TAXONOMY AND PHYLOGENETIC SYSTEMATICS OF THE INDO-PACIFIC WHIP-TAILED STINGRAY GENUS *Himantura* MÜLLER & HENLE 1837 [CHONDRICHTHYES: MYLIOBATIFORMES: DASYATIDAE]

by

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A dissertation submitted to the School of Zoology, University of Tasmania,
in partial fulfilment of the requirements for the Degree of
Doctor of Philosophy (Zoology).

May 2004

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Ph.D.
2004

Declaration and Statement

I hereby declare that this thesis contains no material which has been accepted for the award of any degree or diploma in any university and that, to the best of my knowledge, this thesis contain no copy of previously published material except where due reference is made in the text.

The work reported in this thesis was carried out by myself (B.M. Manjaji) under the supervision of Associate Professor Dr. Robert W.G. White, Dr. Peter R. Last, Mr. Adam J. Smolenski, and Associate Professor Dr. Annadel S. Cabanban, with support from a two-year scholarship granted by the Universiti Malaysia Sabah, and a further two-year scholarship granted by the University of Tasmania and the Sharks and Rays of Australia (SAROA) Project Fund from the Commonwealth Scientific and Industrial Research Organization (CSIRO), awarded to the student.

The commencement of the study was made possible with additional support and services including the use of collection materials, laboratory, computing and library facilities at CSIRO Marine Research Division in Hobart.

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Sincerely,
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CHAPTER 1

1.0 GENERAL INTRODUCTION

The whip-tailed stingrays, genus *Himantura* Müller and Henle 1837, consists of marine, brackish, and fresh water species, and are found in the Atlantic, Indian and Pacific Oceans (Nelson 1994). Their distribution is however, confined to tropical and subtropical waters, with most species known only from a limited range (Compagno & Cook 1995; Compagno & Roberts 1982; Last & Stevens 1994; Zorzi 1995). Coastal stingrays primarily occupy demersal habitats, with many species occurring in aggregations indicating their social nature (e.g. Homma *et al.* 1994).

Over 62 species of stingrays are recognized, and these are grouped into 5 or 6 genera in the Family Dasyatidae (Compagno 1999a). More than a third (23 species) are currently designated as *Himantura* (Compagno 1999a). Preliminary investigations on extant members of the genus have revealed significant morphological diversity, even if they are superficially similar in appearance. These characters include variability in disc shape, size at maturity, tail structure, and squamation (P. Last pers. comm.).

Compagno (1999b) concluded that members within the Order Myliobatiformes, are monophyletic despite being a diverse group. This decision was based on his earlier studies (Compagno 1973, 1977), and is also supported by other more recent morphologically-based phylogenetic studies (Nishida 1990; McEachran *et al.* 1996). Molecular-based studies have only been carried out to investigate the interrelationships between members of the family (Sezaki *et al.* 1999; Chen *in press*). Most other inferential studies utilising methods such as cytotaxonomy (Schwartz & Maddock 1986; Stingo & Capriglione 1986; Stingo *et al.* 1989) and molecular genetics (Dunn & Morrissey 1995; Kitamura *et al.* 1996) were concerned only with the interrelationships of higher taxa, i.e. supporting morphological studies (White 1936, 1937; Holmgren 1942; Compagno 1973, 1977; Schaeffer & Williams 1977; Maisey 1984) of the diphyletic hypotheses on galeomorph and batomorph phylogenies. Nominal species from fossil records have not contributed much to a broader understanding of elasmobranch interrelationships. These seem only to be useful in the revision of sub-ordinal and familial groups that were first established in the 19th century and have been accepted ever since (Maisey 1984).

The structured uncertainty within the Family Dasyatidae is hypothesized to be a reflection of their non-monophyletic interrelationships, as expressed by, for example, Last (1979, 1987), and Compagno and Roberts (1982). Observations of poly- and para-phyletic interrelationships within several of the genera are also being supported by studies on batoid interrelationships (Lovejoy 1996; McEachran *et al.* 1996, Lovejoy *et al.* 1998; Rosenberger 2001a). The results of molecular-based studies are conflicting, with one study less conclusive about the generic monophyly because of low bootstrap support on consensus trees (Sezaki *et al.* 1999), although another study supports generic paraphyly (Chen *in press*, abstract only).

The hypothetical relationship from older classifications appears to be based only on external similarity. Therefore the findings in recent studies of the non-monophyly of the dasyatids are not at all surprising. Maisey (1984) and McEachran (1990) first revealed that the lower level (generic and specific) classification currently in use was never critically reviewed. The taxonomic confusion surrounding dasyatid stingrays was also highlighted by Last and Stevens (1994) where they acknowledged the currently poor species-level taxonomic knowledge, particularly of the stingrays of the Indo-Pacific region. This is illustrated by the inconsistent usage of generic terms for the whip-tailed stingrays which can be found even in recent major publication, such as the Food and Agriculture Organisation (FAO) fisheries identification guide (e.g. Rainboth 1996), as well as the misidentification of some species (e.g. Mohsin & Ambak 1996).

During a survey on elasmobranch biodiversity in Sabah, Malaysia (Fowler *et al.* 1999; Manjaji 2002a, b), similar problems regarding the nomenclature of species were faced. In presenting the findings of the survey, it was mentioned that the names of some of the ray species are provisional, as several species remained unidentified. This appears to be a better way of dealing with nomenclatural problems, and avoids creating further confusion with species identity.

P. Last (pers. comm.) has observed that the decrease of species diversity in fishery catches across the tropics coincided with the absence of batoids in the catch. He postulates that the demise of the predatory batoid fauna is an indicator of the health of the marine coastal community, which in turn acts as an indicator of the general state of the local fisheries. The threats faced by freshwater sharks and rays in their more restricted environment was also highlighted by Compagno and Cook (1995).

The population status of elasmobranchs (including stingrays) in most regions is unknown (Camhi *et al.* 1998). The low economic emphasis placed on this group of fishes means that they are one of the least addressed in fishery resource management (Camhi *et al.* 1998). Catch-effort data from fisheries are also virtually absent (Bonfil 1994), or if available are lumped under the heading 'shark and ray' (e.g. Annual Fisheries Statistics Report by the Sabah Department of Fisheries). Whilst the stingray species previously listed as threatened have now been excluded from the list in the latest IUCN Red List of Threatened Species (Hilton-Taylor 2000), this primarily reflects the lack of data available for the group when using new quantitative criteria (Fowler 2000).

No doubt, one of the confounding problems faced by researchers of the late 18th, 19th and even mid-20th century was communication. Because of this, scientists and other workers in the field were not able to easily share their findings, and this is thought to have contributed to a large species synonymy. It is worth noting, though, that one of the major revisionary works contributing to the current state of flux in stingray taxonomy was that of Fowler (1941). Fowler's poor appreciation of the diversity of the group apparently caused him to lump many valid species together. Many workers dealing with other groups of fishes had complained about the problems created by Fowler as a result of his contributions. Examples are Boeseman (1964) on his notes of the fishes of western Papua New Guinea, and Allen and Talbot (1985) in their revision of the snappers.

One of the other major obstacles faced by researchers in dealing with the taxonomy of the whip-tailed stingrays is the difficulty in obtaining, or even saving study material. Several dasyatids are smallish species with less than 30 cm in maximum disc width, but the majority are large, whose disc widths exceed 1 m and even reach up to 2 m as adults. Even when they reach about 0.5 m across the disc, they are very large. The sharp and coarse dermal denticles on the dorsal surface of the disc and on the tail makes handling, and/or transporting them intact more difficult and even hazardous, and several people are required to move them. The selection of good specimens, particularly of adults, is usually hampered by this factor. As a result of their large size, they are often poorly represented in museum collections.

A full review of this family is clearly warranted, as the taxonomy is so confused, and there is a need to enhance descriptions. One of the difficulties with taxonomic revision of this genus is the accessibility of type specimens, and in accessing original descriptive papers. As mentioned earlier, most of the work carried out was more than a century ago, type specimens are often in a poor state of preservation, have been lost, or are otherwise not accessible. The publication and documentation of these works are often found in the 'Special/Rare Collection' in a small number of libraries in and outside of Australia and even obtaining photocopies is often difficult. Moreover, several of these fundamental works were written in languages other than English, and much effort has to be spent to gain translations.

It is the aim of this study to taxonomically review the group. The scope of study had to be limited to one of the extant genera; *Himantura* Müller and Henle was selected. Stingrays currently grouped under this genus are the most abundant form found in tropical waters of the South China Sea (Fowler *et al.* 1999; Fowler *et al.* 2002; Last & Compagno 1999), with current figures suggesting between 20-23 species (Compagno 1999a). The relative abundance of this group, particularly from fish markets of the Malaysian state of Sabah, meant that it was relatively easy to access and obtain specimens required for this study, which are otherwise lacking in existing collections.

The main objective of this study is to phylogenetically classify members of this genus that are currently grouped solely on the absence of a skin fold on the tail, and to document morphological variation of extant taxa. As a first approach, extant taxa were grouped into several species complexes based on their synapomorphies, or general external similarity. However, it is emphasized that this did not influence the cladistic (morphological) analysis with *a priori* assumptions of character polarity. Character polarity was resolved by rooting the resulting tree, rather than before a tree was generated (Nixon & Carpenter 1993).

Following this introductory chapter, this thesis includes two main sections, a general discussion, and conclusion. In Section 1 (Systematics), taxonomic methods for the taxonomic revision are outlined in Chapter 2, and character analysis for the morphological phylogenetic inference outlined in Chapter 3. The application of molecular techniques (DNA sequencing using Polymerase Chain Reaction) for phylogenetic inference is given in Chapter 4. In Section 2 (Taxonomy), a taxonomic account, including a key to species and species description of the Indo-Pacific whip-tailed stingray based on the results of Chapters 3 and 4 in Section 1, is given (Chapter 5). A general discussion (Chapter 6) and conclusion (Chapter 7) is based on the overall result of the study. Except for Chapter 2, each chapter under the main sections are self-contained in that the results and discussion are given under the same chapter heading.

The thesis is presented in two volumes, and combined into one bound copy: Volume I contains Chapters 1-4; Volume II contains Chapters 5-7, References, Tables (if not already included in the text) and Appendices. References are cited following the *Academic Press* format.

CHAPTER 2

2.0 TAXONOMIC REVISION

Taxonomic accounts of whip-tailed stingrays genus *Himantura* of the Indo-Pacific region dates back to the late 18th century until the present time (e.g. Forsskål 1775; Rüppell 1835; Annandale 1909; Roberts & Karnasuta 1987). The contribution to the knowledge of whip-tailed stingrays in this region can be largely attributed to the dedicated works of Bleeker (1851, 1852, 1856, 1877), in particular. Many of the other early works were the result of numerous ichthyological surveys conducted within the region. For example, an in-depth historical account of such surveys by European, American and Australian researchers within the New Guinea sub-region alone has been documented by Munro (1967).

Nevertheless, despite over 200 years since the first admissible work (ICZN 1999) describing a stingray from the Red Sea (Forsskål 1775), published taxonomic accounts of the group are relatively few when compared to that of other batoid groups, especially the skates (Stehmann 1971), and to a lesser extent, the electric rays (Carvalho 1999). Confusion currently exists as to species identity for a large number of species within the whip-tailed stingrays.

Early major revisionary works on the group by Garman (1913) and Fowler (1941) had a poor appreciation of the diversity of this group. The reliability of many early revisions is also questionable as these were much influenced by the absence of representative material of each species (Last 1979). Nevertheless, Garman's and Fowler's works provides a wealth of information on nominal taxa and referencing, and are often cited and recognized as a fundamental basis for future revisionary works and/or compilations as well as character examination for phylogenetic studies (e.g. Jordan 1923; Bigelow & Schroeder 1953; Compagno & Roberts 1982, 1984; Lovejoy 1996; Mould 1999).

The current state of flux of species identification is partly contributed by authors who have inadequately described the species. Many early descriptions constituted very brief, three- to four-sentence paragraph often describing the most conspicuous characteristic and, without any accompanying illustrations, it is left to the imagination of the reader to picture what was being described. Furthermore, in most cases, new stingray species were described from poorly preserved and/or only part of a specimen, such as from a dried tail (e.g. *Trygon atrocissimus* Blyth 1860).

To date, the most comprehensive treatment of Indo-Pacific whip-tailed stingray species is by Last and Stevens (1994), which included species accounts of sharks and rays from tropical waters of Australia. The restricted range of most whip-tailed stingrays (Last & Stevens 1994; Compagno 1999c) however, means that many species are not accounted for in works such as this. Hence, the published information, and in particular the description of other extant species, remain scattered in the form of individual papers (e.g. Sauvage 1878; Compagno & Roberts 1982).

The Australian shark and ray volume was later adapted for a chapter in a guidebook to species occurring in the Western Central Pacific (Last & Compagno 1999). Although many of the other species were listed in the guide, information about these species is very limited, i.e. apart from an illustration depicting a particular species and its known distribution, no descriptive characters were provided. This reflects the need for a thorough taxonomic review of the group, as acknowledged by the authors themselves, and by other authors working on higher level systematics (e.g. Maisey 1984; Lovejoy 1996).

Taxonomic work presented by various authors reflects the lack of a standard taxonomic method for the whip-tailed stingrays, and in particular, the description of disc shapes, morphometrics and count procedures. As a result, there is a plethora of (synonymous) descriptive terminologies in current usage. However, in most cases, the disc shape is inadequately described. There are also many measurement procedures which have been proposed for other groups, namely the skates (Hubbs & Ishiyama 1968). The lack of a consistent method for data acquisition among different workers makes data comparison almost impossible, and unnecessarily time consuming (see also Compagno *et al.* 1990).

The importance of a standardized taxonomic method is much emphasized in view of the paucity and difficulty in obtaining study materials, especially for this batoid group. As previously mentioned in Chapter 1, it is the sheer size that some dasyatids can reach which makes them difficult to study.

One of the main tasks when describing a new species is their generic allocation (Hennig 1979). However, most of the batoid genera do not have a complete description and many of the types are missing or misplaced. Additionally, most were introduced primarily to serve a purely Linnaean system of classification. The principle of this method of classification may be referred to what McEachran (1990) termed the 'hangover belief', in which taxa are classified as mutually exclusive sets either possessing or lacking a particular character.

In the case of *Himantura*, the key character to this genus has somehow been singled out as 'the absence of a tail skin fold'. The trend for using this character can be traced back to Garman (1913), who himself had probably adopted this character from the description of the type species, *H. uarnak* (Forsskål 1775). The presence of a skin fold on the tail would otherwise place a species in either one of three other genera of the Dasyatidae, most likely within *Dasyatis*, as the other two genera (i.e. *Pastinachus* and *Pteroplatytrygon*), are monotypic (e.g. see Compagno 1999a, b).

It is only recently, within the last decade, however, that the robustness of the tail skin fold character was tested, using phylogenetic analyses of both higher and lower level batoid interrelationships (Nishida 1990; Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a). There is considerable disparity among these studies in coding for this character, mainly due of the differences in selection of the Operative Taxonomic Units (OTUs), including outgroups. Nevertheless, the general consensus is that the tail skin fold character alone did not form a basis for resolution of the interrelationship between *Himantura* and *Dasyatis*. None of the studies mentioned above proposed any generic reassignment of the respective species analysed. Instead however, non-congeneric species are conveniently distinguished using regional prefixes pending further revision of the group. An example is the use of

'Indo-Pacific' and 'amphi-American' to distinguish *Himantura* from both regions (Lovejoy 1996).

Many batoid taxonomists have, in fact, recognized the problem of using the tail skin fold character long before any phylogenetic analyses has been carried out (e.g. Compagno & Roberts 1982; Last 1987; Nishida & Nakaya 1988a; Last & Stevens 1994), which, as a result saw only the tentative allocation of a newly described species to either *Himantura* or *Dasyatis*. In the meantime, taxonomists continue to allocate newly described species using the tail fold character, in anticipation of a much needed review of the group (e.g. Gomes *et al.* 2000; Rosa *et al.* 2000).

The aim of this chapter is the methodological standardization for the alpha taxonomic revision of Indo-Pacific whip-tailed stingrays that are currently designated under the genus *Himantura* Müller and Henle 1837. The monophyly of the genus is then tested and the relationship between extant taxa estimated, using both cladistic (morphological) and molecular phylogenetic methods by outgroup analysis. Therefore, the taxonomic accounts (Volume 2, Section 2, Chapter 5) are presented after the phylogenetic systematic analyses (Volume 1, Section 1).

2.1 MATERIALS AND METHODS

2.1.1 Materials

Specimens examined comprised all known species from tropical to subtropical Indo-Pacific region (Last & Stevens 1994; Compagno 1999b; Last & Compagno 1999). This includes several undescribed species discovered during the course of this study. Materials examined were in the form of fresh and preserved whole and/or parts of a specimen, photographs and radiographs. An important collection of rays was obtained during a field trip to the Malaysian states of Sabah and Sarawak between February and May 1999. Except for the giant river whip-tailed stingray, all sampling were made in the various coastal fish markets, which were also the fish landing points. Specimens of the river ray which apparently never or only very rarely reach the fish markets, were obtained through local contacts established during an earlier project (Fowler *et al.* 1999; Fowler *et al.* 2002), mainly villagers living along the Kinabatangan River. In addition, tissues for molecular studies (Chapter 3) were sampled from freshly killed rays before other data were extracted. A flowchart of the market sampling strategy is given in Appendix 2.1.1.

The effort to examine type materials proved to be a daunting task. Most types were unavailable for loan, the primary reason being the fragility of these specimens (dried and mounted), many of which are between 100 to 200 years old. However, most museums also have a policy of not transporting type materials through the mail, although these may be made available for loan if they were to be hand-carried. A limited time-frame and insufficient funding during this study meant that visits to the museums to personally examine type materials were not possible. In such cases, the assistance from staff of the respective museums, and from colleagues who have access to the museum materials were sought to obtain the relevant information. This includes morphometrics, observations on squamation, and taking photographs and radiographs. Explicit instructions on the methodology as devised in this study, were given to the trusted colleagues. All assistance received is duly acknowledged in the following chapters.

Other available non-type (preserved) museum materials were also examined and radiographed when possible. Information on skeletal structures was further obtained by limited dissections of representative specimens, subject to availability of specimens. Type specimens were not normally dissected, except for specimens of two new species discovered during the course of this study.

Most of the specimens collected, including others obtained by donation from various sources, were deposited at the I.S.R. Munro Ichthyological Collection, CSIRO Division of Marine Research, Hobart. Other specimens from the same batch collected from Malaysia were deposited at the Borneo Marine Research Institute, Universiti Malaysia Sabah (Kota Kinabalu). These are mostly large specimens too bulky and costly to transport overseas. All these were examined and included in the materials examined, but not all have been registered as of the end of the writing of this thesis. Other unregistered specimens included those examined at the Sabah State Museum (Kota Kinabalu), materials on loan from Silliman University Marine

Laboratory (Dumaguete), and photographs of unregistered materials in the *Lembaga Ilmu Pengetahuan Indonesia* (Muara Angke). Unregistered materials are listed according to their field codes with the appropriate prefix, and presented in the following, together with other recognized museum and institutional codes (Leviton *et al.* 1985; Leviton & Gibbs 1988; Kottelat *et al.* 1993). Materials examined are listed in Appendix 2.1.2, and are also given under the respective species heading.

Code	***Institution, City***
AMS	Australian Museum, Sydney
BMNH	Natural History Museum, London
BPBM	Bernice P. Bishop Museum, University of Hawaii, Honolulu
CAS	California Academy of Sciences, Department of Ichthyology, San Francisco
CSIRO	I.S.R. Munro Ichthyological Collection, Commonwealth Scientific and Industrial Research Organisation (CSIRO) Division of Marine Research, Hobart. (This is the same collection listed as CSIRO Fisheries and Oceanography, New South Wales by Leviton *et al.* 1985. It was moved to the current location in Hobart in 1985 shortly after publication of the paper [A. Graham, pers. comm.]).
HUMZ	Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate
LACM	Natural History Museum of Los Angeles County, Los Angeles
LIPI	Lembaga Ilmu Pengetahuan Indonesia, Muara Angke
MNHN	Muséum National d'Histoire Naturelle, Paris
MTUF	Museum of Fisheries Science, Tokyo University of Fisheries, Tokyo
NMV	National Museum of Victoria, Melbourne
NTM	Northern Territory Museum of Arts and Sciences, Darwin
QM	Queensland Museum, Brisbane
RMNH	Nationaal Natuurhistorisch Museum, Leiden
ROM	Royal Ontario Museum, Toronto
SMF	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt
SMKK	Sabah State Museum, Kota Kinabalu
SUML	Silliman University Marine Laboratory, Dumaguete
UMS	Borneo Marine Research Institute, Universiti Malaysia Sabah, Kota Kinabalu
USNM	National Museum of National History, Smithsonian Institution, Washington D.C.
WAM	Western Australian Museum, Perth
ZRC	Zoological Reference Collection, Raffles Museum, University of Singapore, Singapore

2.1.2 Morphological methods

2.1.2.1 Disc shape

The pectoral disc, commonly referred to as the 'disc' of batoids is essentially formed from the enlarged pectoral-fins that are directly united with the depressed head and trunk. The description of the disc shape based on its general outline alone, as is commonly practised, is considered rather vague without the description of its attributes. This is in view of the different terminologies adopted by different authors to describe a basic shape, and the fact that many rays are not necessarily readily categorized into a certain shape. For example, when the disc is simply described as 'diamond-shaped' and 'rhomboidal', the fact that a ray may have a more angular snout or a more broadly rounded pectoral-fin apex is not accounted for. Detailed description of a disc shape is further emphasized in that each of these attributes represents a potential homologous character for phylogenetic analyses (Chapter 3). Thus, while it is recognized that authors may continue to use different terminologies for describing a particular disc shape, there should be a standard method as to how the disc is described.

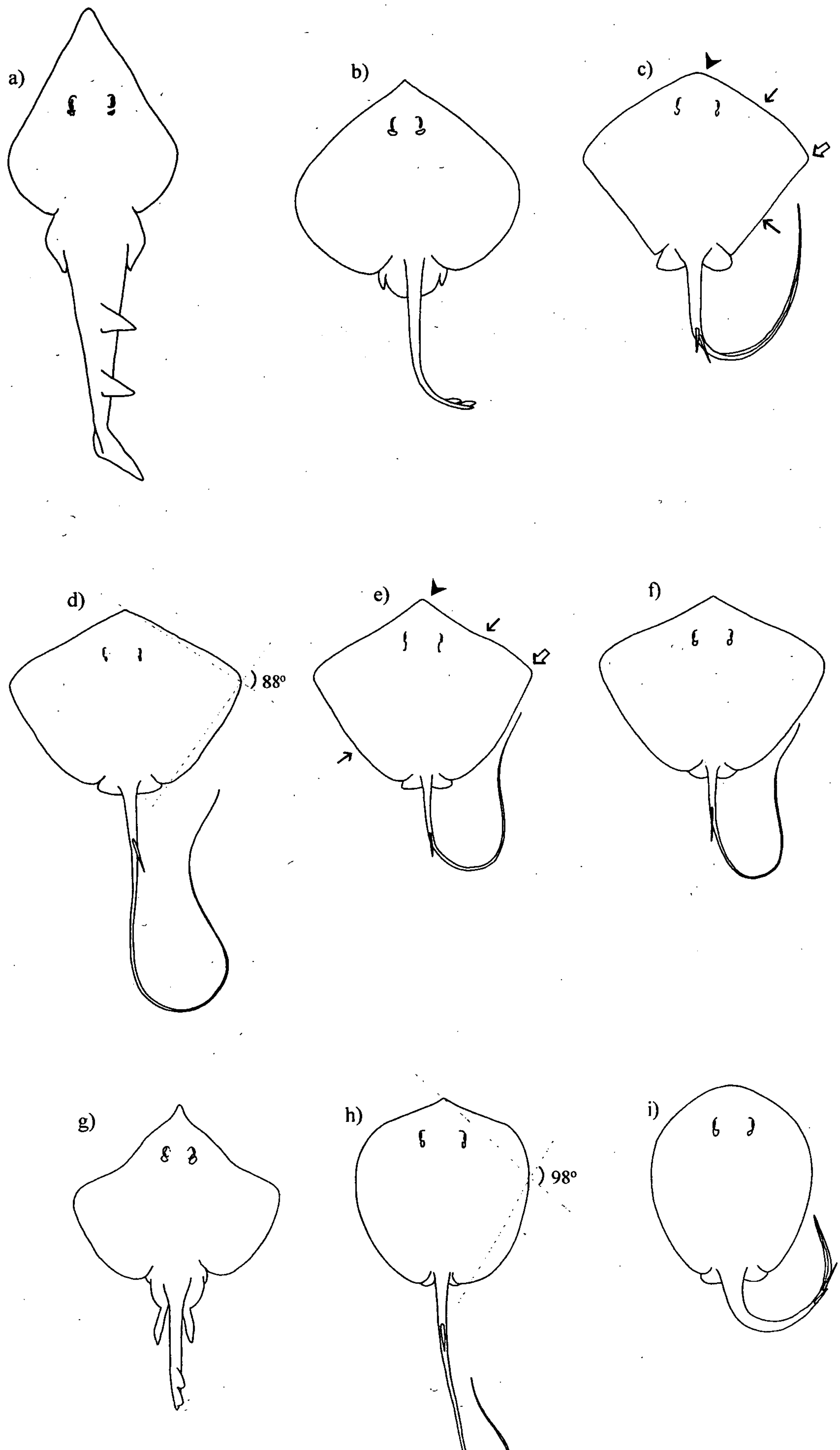
Three main attributes of the disc recognized herein are the snout, lateral apices and disc margins. These attributes all contribute to the various transitional forms seen in the disc shapes of batoids. To demonstrate the various forms displayed by these main attributes, the disc shapes of all known batoids are considered in this assessment. The method proposed herein is applicable for all batoids. Based on the diversity in the shapes of the discoid rays (see Last & Stevens 1994), these are broadly categorized into six types, i.e. wedge-shaped, heart-shaped, rhomboidal, oval, circular, and lozenge-shaped (Figure 2.1.1).

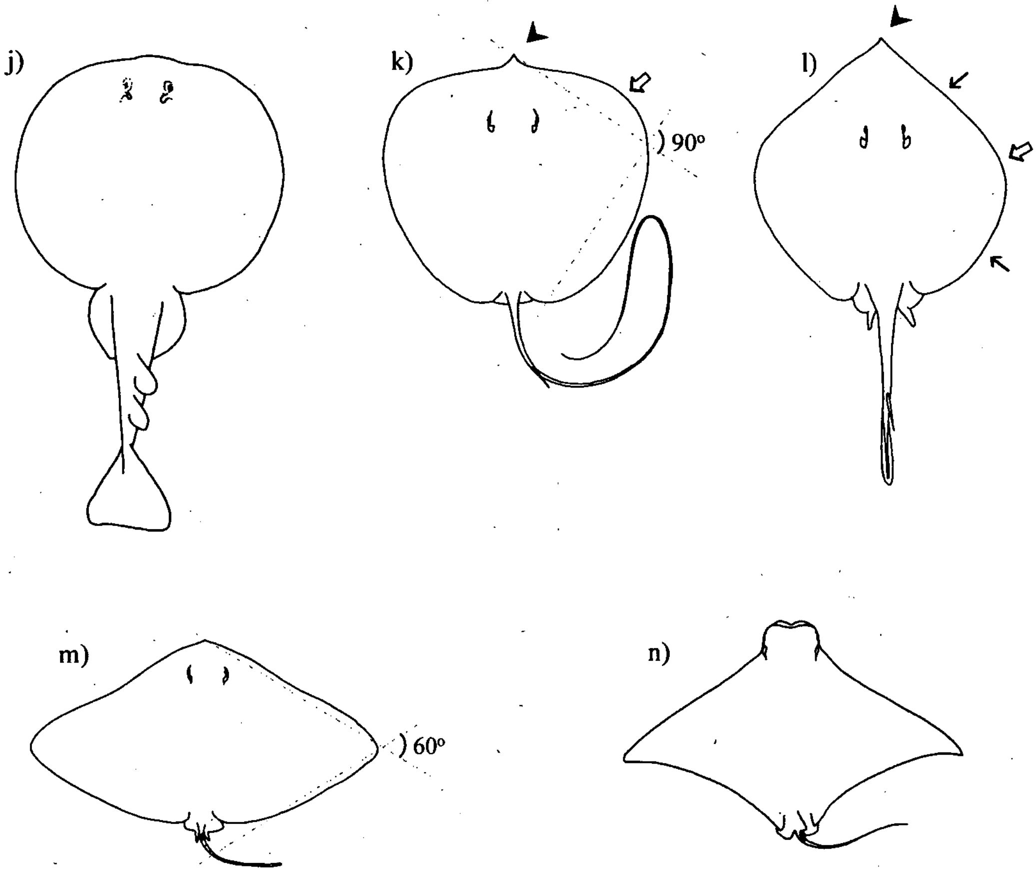
The snout is described by its length, angularity at the snout tip, and whether a lobe at the snout tip is present or absent. The length of the snout may be justified by a measure of quantification, e.g. 'times in eye length'. The snout angle is often measured as the angle between two lines at the tip of the snout, projected to the anterior margins of the disc where it crosses the horizontal preorbital length (see section on morphometrics, this chapter). Thus, description of the snout of two sub-circular rays is exemplified by, 'anteriorly truncated, small triangular lobe present at snout tip, snout angle 113-117°, broad based, snout extremely elongate (about seventeen times eye-length)' for the giant river stingray *Himantura chaophraya* (Figure 2.1.1k), or, the snout may be described as, 'snout angle 97-104°, broad based, rather elongate (about nine times eye-length), lobe present at snout tip' for the giant stingaree *Plesiobatis daviesi* (Figure 2.1.1l).

The lateral apices of the disc, or the pectoral-fin apices, are variably shaped from being narrowly to broadly rounded, or from narrowly to broadly angular, and are positioned at a level either more anteriorly nearer to the snout tip, or about halfway between the anteriormost and posteriormost points of the disc. Where authors have described the shape of the pectoral-fin apices, the description of the angularity is often subjective. A method to measure the angle of the pectoral-fin apex is hereby proposed. By projecting an imaginary line, each from the snout tip and from the free posterior tip of the disc to a point on the lateral margin where the disc is widest, the crossing of the two lines is measured as the angle of the pectoral-fin (see Figure 2.1.1). Therefore, as with the snout, the degree of angularity of the pectoral-fin apex can be quantitatively expressed.

The values obtained are used in combination with the lateral position of the pectoral-fin apex to describe its degree of angularity. In this study, I chose several values as the standard to draw a line between the term 'acute' (narrow), 'moderate' and 'obtuse' (broad), based on the measurements outlined earlier. The pectoral-fin apex is considered 'acute' if it is 70° or less, 'moderate' if between 70 °-90°, and 'obtuse' if more than 90°. Thus, as an example, the pectoral-fin apices are acutely angular in the Australian butterfly ray *Gymnura australis* (Figure 2.1.1m) and the Australian cownose ray *Rhinoptera neglecta* (Figure 2.1.1n), moderately angular in the pink whip-tailed stingray *H. fai* (Figure 2.1.1d) and in the adult form of the reticulate whip-tailed stingray *H. uarnak* (Figure 2.1.1f), and obtusely angular in the mangrove whip-tailed stingray *H. granulata* (Figure 2.1.1h). The pectoral-fin apices of *H. chaophraya* (Figure 2.1.1k) are obtusely rounded with their position far forward of the disc, and the disc with a truncated snout.

Figure 2.1.1. Outline illustration of seven broad categories of disc shapes in batoids. a) wedged-shaped (e.g. *Rhinobatos typus*), b) heart-shaped (e.g. *Notoraja* sp.), c-g) rhomboidal (e.g. c- *Dasyatis kuhlii*, d- *Himantura fai* , e- *H. toshi*, f- *H. uarnak*, g- *Raja australis*), h-i) oval (e.g. h- *H. granulata*, i- *Taeniura lymma*), j-l) circular to subcircular (e.g. j- *Torpedo* sp. A, k- *H. chaophraya*, l- *Plesiobatis daviesi*), m-n) lozenge-shaped (e.g. m- *Gymnura australis*, n- *Rhinoptera neglecta*). Arrow-heads and arrows indicate reference to the snout (➤), pectoral-fin apex (⇨) and disc margins (→). Images redrawn from Last & Stevens (1994).


a)
b)
c)
d)
88°
e)
f)
g)
h)
98°
i)


j)
k)
90°
l)
m)
60°
n)

The description of the disc margin is based on whether it is concave, convex, or straight. Describing the disc margin is particularly useful in distinguishing two rays with a very similar disc shape. For example, both the blue-spotted maskray *Dasyatis kuhlii* (Figure 2.1.1c) and the black-spotted whip-tailed stingray *H. toshi* (Figure 2.1.1e) although having similar disc shape, as well as similar in two (i.e. snout and pectoral-fin apex) of the three disc attributes, the disc margin attribute is dissimilar between the two species (i.e. being anteriorly convex and posteriorly straight in the former, compared to anteriorly concave and posteriorly convex in the latter).

2.1.2.2 Morphometrics

Morphometrics were obtained from the left side of a specimen in its normal resting position whenever possible. However, reliable measurements could not be taken from damaged or distorted preserved specimens. This was the case for many of the older type specimens, some of which were stuffed and dried. Measurements were taken as standard direct lengths (shortest point to point distance) (Last & Stevens 1994), except for the distance from the snout tip along the midline of the disc to a perpendicular line joining the eyes. Small specimens and lengths of up to 300 mm were measured using electronic and manual callipers; otherwise, a mounted board ruler was used to measure larger specimens. In some instances, a custom-made wooden divider was used as an aid to measure disc width and length, and total length of large specimens in the markets. A custom-made plastic divider was also used as an aid to measure the thickness of large specimens in the laboratory. Measurements of up to 300 mm were recorded to the nearest 2 decimal points, and measurements exceeding 300 mm were recorded to the nearest millimeter. The measurements are a combination of methods used by CSIRO (P. Last unpublished; pers. comm.), and from published works, namely Hubbs and Ishiyama (1968), Compagno and Roberts (1982), Compagno and Heemstra (1984), and Last and Stevens (1994). The list of measurements was compiled to maximize use of measurable characters. Such a measure is bound to include redundant data, as shown in preliminary analyses of the data. Nevertheless, although the redundancy of data is specifically not useful for comparative studies, these are still useful for species description purposes, and hereby proposed as the basis for standard measurement in whip-tailed stingrays.

The following are the measurements (Figure 2.1.2) and their abbreviations, listed in the order they are taken, which was designed so as to minimize handling of specimens.

1. Snout angle (SA): is the angle measured at the apex of the snout projected to the width of the disc in horizontal preorbital length (Fischer & Hureau 1987).

2. Disc thickness (DT): greatest thickness of disc, at or near scapulocoracoid. The thickness of the midscapular denticle was not included in the measurement of disc thickness.

3. Total length (TL): distance from tip of snout to tip of tail.

4. Disc length (DL): distance from snout tip to the pectoral-fin free rear tips.

5. End of orbit to pectoral insertion (OP1): distance from posterior edge of orbit to insertion of pectoral-fin.

6. Snout to pectoral insertion (SP1): distance from snout tip to pectoral-fin insertion.

7. Disc width (DW): widest point of disc from left to right.

8. Snout to maximum width (SW): perpendicular axis from snout tip to line of greatest disc width.

9. Snout, preorbital (direct) (SD): distance from snout tip to anterior margin of orbit.

10. Preorbital (horizontal) (SH): distance from the snout tip along the midline of the disc to a perpendicular line joining the eyes.

11. Orbit diameter (OD): longitudinal length of the (protruding) fleshy eyeball.

12. Eye diameter (ED): greatest longitudinal length across the eyeball, including skin covering the eyeball, but not loose surrounding tissue.

13. Spiracle length (SL): greatest longitudinal diameter across the spiracular depression, from inner posterior margin to anteriormost angle beyond opening; calipers are pressed against the skin of the depression.

14. Orbit and spiracle length (OS): distance from anterior edge of orbit to posterior end of spiracle.

15. Interorbital width (IO): least width between inner edges of left and right orbits/eyeballs measured by pressing calipers lightly together, so as to measure width, including the moderately firm underlying tissues, but not necessarily the cartilages.

16. Inter eye width (IE): least width between outer edges of left and right orbits.

Figure 2.1.2a. Dorsal external measurements on an outline illustration of a representative dasyatid. DL- Disc length, DW- Disc width, ED- Eye diameter, IE- Inter eye width, IO- Interorbital width, IS- Distance between spiracles, OD- Orbit diameter, OP1- End of orbit to pectoral insertion, OS- Orbit and spiracle length, P1S- Pectoral insertion to sting origin, S1- Sting 1 length, SA- Snout angle, SD- Snout, preorbital (direct), SH- Snout, preorbital (horizontal), SL- Spiracle length, SP1- Snout to pectoral insertion, SW- Snout to maximum width, TL- Total length, WP2- Tail width, axial of pelvics, WS- Tail width, base of sting. See text for definitions.

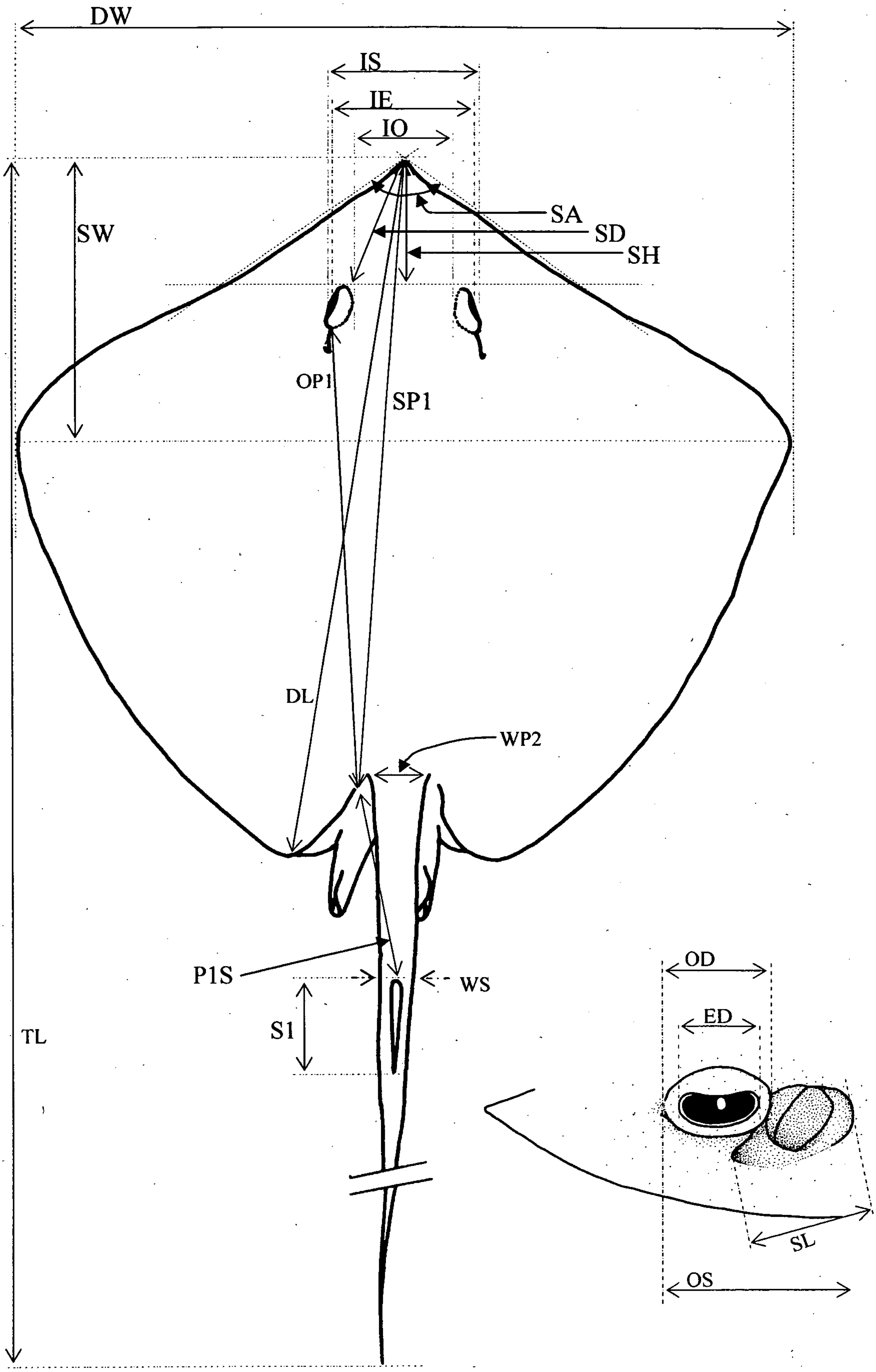
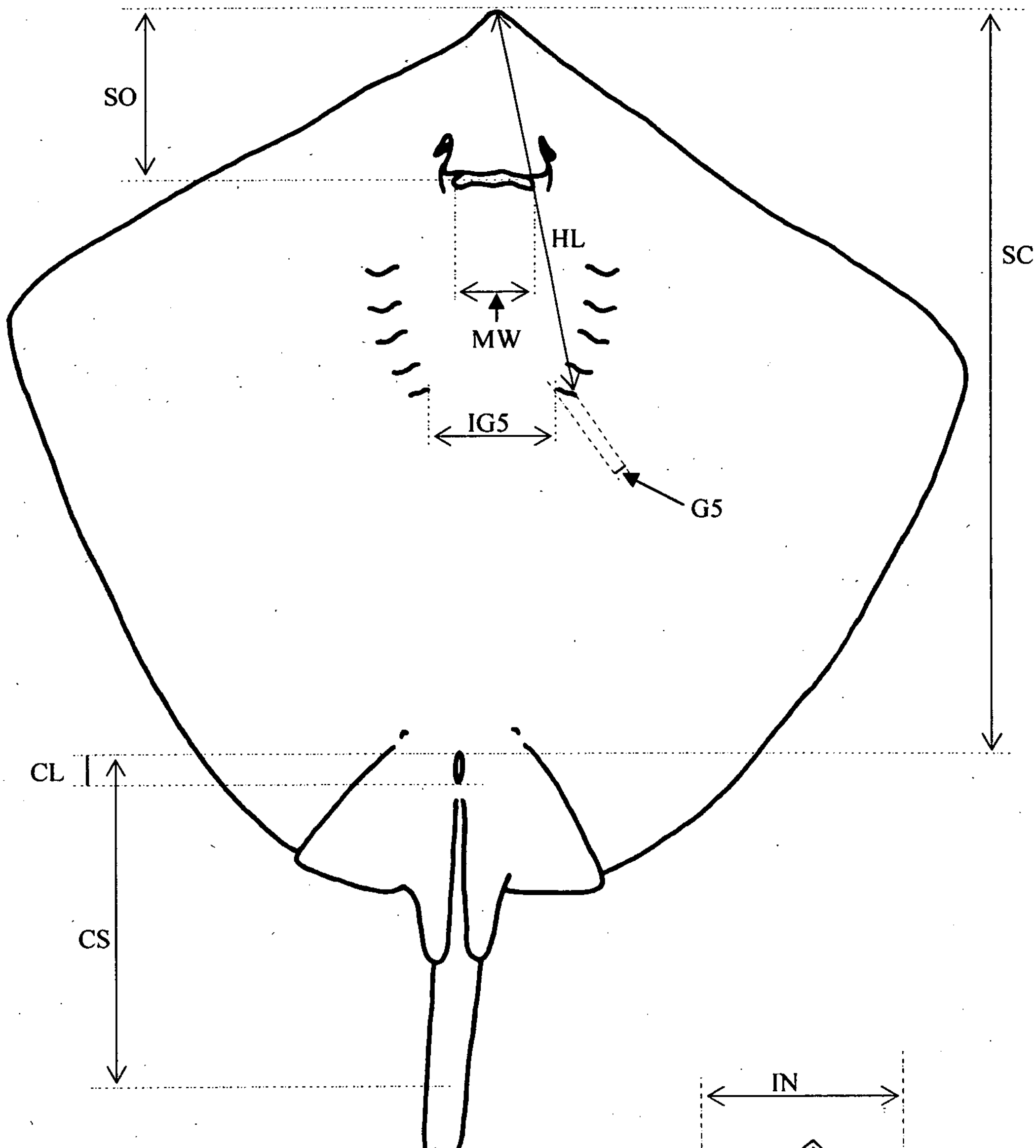
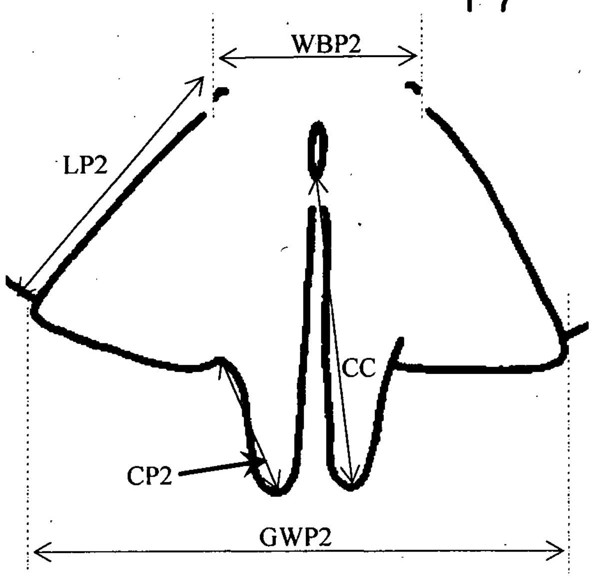

DW
IS
IE
IO
SA
SD
SH
SW
OP1
SP1
DL
WP2
P1S
WS
S1
TL
OD
ED
SL
OS

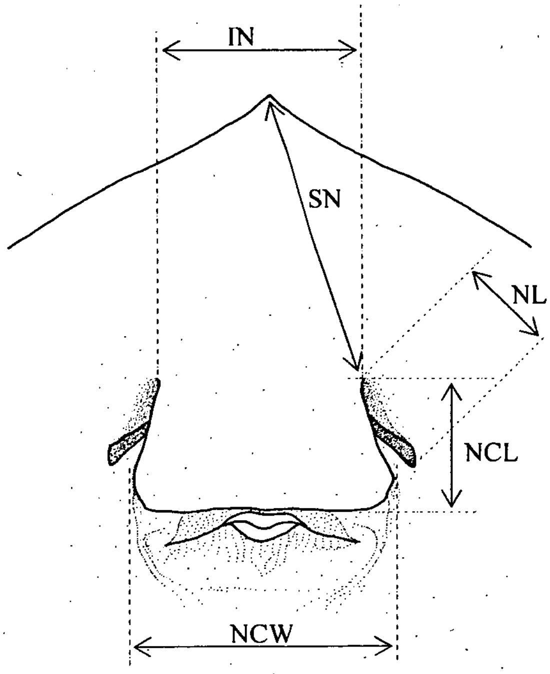
Figure 2.1.2b. Ventral external measurements on an outline illustration of a representative dasyatid. CC- Clasper, postcloaca length, CL- Cloaca length, CP2- Clasper, length from pelvic axial, CS- Cloaca origin to sting, G5- Width of 5th gill slit, GWP2- Greatest width across pelvic fins, HL- Headlength (direct), IG5- Distance between 5th gill slits, IN- Distance between nostrils, LP2- Length pelvic fin, MW- Mouth width, NCL- Nasal curtain length, NCW- Nasal curtain width, NL- Nostril length, SC- Snout to origin of cloaca, SN- Snout, prenasal, SO- Snout, WBP2- Width across pelvic-fin base. See text for definitions.



SO
SC
HL
MW
IG5
G5
CL
CS



WBP2
LP2
CC
CP2
GWP2



IN
SN
NL
NCL
NCW

17. Interspiracular width (IS): least width between inner rims of left and right spiracles.

18. Tail width, base of sting (WS): width of tail at base of sting (if more than one sting, then, base of first (lower) sting).

19. Tail height, base of sting (HS): height of tail at base of sting (if more than one sting, then, base of first (lower) sting)

20. Sting length (S1, S2): distance from its anterior origin on the tail to its free rear tip, respectively.

21. Pectoral insertion to sting origin (P1S): distance from insertion of pectoral-fin to base of sting (if more than one sting, then, base of sting nearest to tail base).

22. Tail width, axial of pelvics (WP2): width of tail at pelvic-fin insertion.

23. Tail height, axial of pelvics (HP2): height of tail at pelvic-fin insertion.

24. Cloaca length (CL): distance from origin of cloaca to inner rim of the posterior end of the cloaca.

25. Clasper, postcloaca length (CC): distance from the outer rim of the posterior end of the cloaca to free rear tip of clasper.

26. Clasper, length from pelvic axial (CP2): distance from its lateral origin on the pelvic-fin to its free tip.

27. Cloaca origin to sting (CS): distance from origin of cloaca to base of sting (if more than one sting, then, base of sting nearest to tail base).

28. Snout to origin of cloaca (SC): distance from snout tip to origin of cloaca.

29. Cloaca origin to tail tip (CT): TL minus snout to origin of cloaca.

30. Length pelvic-fin (LP2): distance from fin origin to its posteriormost tip (pelvic-fin origin or base is appreciable with thumbnail).

31. Width across pelvic-fin base (WBP2): width of the pelvic bar (pelvic-fin origin or base is appreciable with thumbnail).

32. Greatest width across pelvic-fins (GWP2): width across the outstretched apices of the pelvic-fins (fin in its natural position).

33. Width of (1st, 3rd, 5th) gill slits (G1, G3, G5): greatest dimension of the gill slit, respectively.

34. Head length (direct) (HL): distance from snout tip to the outer end of the fifth gill slit.

35. Snout (SO): distance from snout tip to the posterior edge of median tooth band of the lower jaw (mouth in normal closed position, upper and lower jaws in contact).

36. Snout, prenasal (SN): distance from snout tip to the nearest point on the outer rim of the nostril.

37. Nostril length (NL): greatest dimension of the outer rim of the nostril.

38. Nasal curtain length (NCL): distance from the front margin of nostril to rear margin of curtain, including fimbriae of curtain. (When fimbriae are well developed, length of longest is taken.)

39. Nasal curtain width (NCW): greatest width of the posterior free margin of the nasal curtain.

40. Distance between nostrils (IN): least distance between nostrils at sides of nasal curtain.

41. Distance between (1^{st}, 5^{th}) gill slits (IG1, IG5): the distance between the inner ends of left and right first and fifth gill slits, respectively.

42. Mouth width (MW): greatest dimension across the tooth band of upper jaw.

2.1.2.3 Meristics

Meristic data were obtained from radiographs (i.e. pectoral and pelvic pterygia, and vertebrae counts) and from actual counts on the specimens (i.e. tooth, oral papillae and nasal rachi counts). Pterygial counts were made from both sides of a specimen, and the results presented in a range if the number differs, whilst nasal rachi counts were made from the left nostril. Meristic counts follow Compagno and Roberts (1982), with one modification: the position of a radial's base (relative overlap) determines its subpterygial placement when intermediate between the propterygium and mesopterygium, or between the mesopterygium and metapterygium. Tooth row counts for both upper and lower jaws were counted at an angle from one corner of the mouth (e.g. Stehmann *et al.* 1978; Stehmann 1981; Fischer & Hureau 1987). The lower jaw usually had to be slit to reveal teeth at the angle of the jaws. The fine tooth rows of young whip-tailed stingray specimens were sometimes stained to aid counting. This was done by blotting the tooth band with paper tissue soaked in dye (alcian blue). An observation of the number and shape of oral papillae was also made. These were made on both fresh and preserved specimens.

Following are the counts and their abbreviations, listed in alphabetical order:

1. MSR- mesopterygial radials: count starts from the first radial on the mesopterygium; the mesopterygium in some species are divided into two or three smaller segments.

2. MTR- metapterygial radials: count starts from the first radial on the metapterygium to the posteriormost extension.

3. MV- monospondylous vertebrae: the monospondylous separate centra and second synarcual are combined in a single count for all the specimens.

4. preD and postD- prespine and postspine diplospondyous vertebrae: the diplospondyous separate centra usually start at position of the origin of cloaca and this can been observed from radiographs, although may be difficult at times; for most species, the diplospondyous vertebrae ends anterior to the base of sting.

5. PF- oral papillae: number of papillae on floor of mouth.

6. P- palate ridges: number of horizontal ridges on roof of mouth.

7. PR- pelvic radials: count includes all the radials in the pelvic-fin, including the 2 or 3 fused radials in the anteriormost extension; for males, the clasper is not added to the count but presented as a single radial (indicated by a '+1' after the radial count).

8. PRR- propterygial radials: count starts from where the anteriormost extension of the propterygium bifurcates.

9. R- rachi: number of oronasal folds.

10. TR- total pectoral radials: total count of the PRR, MSR, and MTR.

11. TV- total vertebrae: total count for monospondylous and diplospondyous vertebrae, '+ 1' (indicating the long unsegmented notochordal sheath beyond the sting.)

12. UTR, LTR- upper and lower tooth rows: rows counted at an angle from a corner of the mouth. (the lower jaw had always had to be slit to be able to count the tooth rows).

2.1.2.4 Squamation

Terminology of dermal structures and their arrangement

The term denticle is herein used to refer to the smaller or moderately-sized placoid scales, typically for those less than 4 mm in diameter. On the other hand, placoid scales larger than 4 mm in size are referred to as thorns. The general structure plan of the placoid scale consists of three parts: a crown attached by a pedicel to a spreading basal plate (Applegate 1967). For a denticle, the three parts may be more readily distinguishable, whilst for a thorn, a pedicel (or neck) is not clear, the crown and the enlarged basal plate usually appear to be directly joined (Reif 1979). Other specific terms referring to the structures on denticles, follow Deynat and Séret (1996) and Deynat (1998), where applicable. The term sting is used to refer to the stinging spine(s).

The term 'denticle' is also used to generally refer to both denticles and thorns arranged in a band, as in 'denticle band', unless otherwise specified. Denticles in the Indo-Pacific whip-tailed stingrays are confined to the dorsal surface of the disc, although these may be present on the entire surface on the tail. Preliminary examinations suggest a fairly conserved pattern in denticle arrangement, as that reported in sharks (Applegate 1967), and in other ray taxa (e.g. Deynat 1998).

The presence of a series of spiny denticles on the marginal edge of the disc of most of the Indo-Pacific whip-tailed stingray is reported for the first time. This series consists of minute denticles with uniform shape and size, and exist as a very narrow band with no immediate adjacent denticles. Their microscopic size (<1 mm), means they are more readily observed under magnification. Following Deynat's (1998) method of thorn series terminology in rajoids, this denticle series is termed 'posterolateral series', as these occur along the posterior margin of the disc.

Denticle shapes in whip-tailed stingrays

The denticle shapes of the whip-tailed stingrays are categorized into six types, as depicted in Figure 2.1.3. Each of these generalized forms is described in this section, as they will be used in the species descriptions. It is noted that in addition to these shapes, there are other shapes in existence. An example, is the conical denticles with stellate bases as shown in Compagno and Roberts (1982). For each of these shapes, every other possible gradient of shapes and sizes was observed. For example the crown of the conical denticles may be more pointed or that its surface is ridged. Many other shapes also exist (e.g. Deynat 1996, 2000) but are not found in the whip-tailed stingrays (this study). However, the examination of all denticle shapes and types in batoids is beyond the scope of this study, although, it is considered appropriate to borrow the established terminologies, where applicable.

Seed-shaped denticles are typically seed-like in appearance, with an actual size (anterior-posterior) not exceeding 2 mm. They are characterized by an anteriorly rounded and posteriorly blunt pointed ends, whose crown is flat to slightly convex, and embedded basal plate. This denticle shape is confined to the scapular area. (Figure 2.1.3a).

Lanceolate-shaped denticles are largish elongated denticles, with an actual size usually exceeding 2 mm in anterior-posterior length. The anterior end is variably slightly indented to truncated, but sharply pointed posteriorly. The crown is slightly concave, its prominent free posterior tip projected dorso-posteriorly. The basal plate is sloped, posteriorly almost twice as thick as anteriorly. This denticle shape is readily observed along the trunk, above the abdomen, and along the mid-dorsal surface from the tail base to the sting base. (Figure 2.1.3b).

Ovate-shaped denticles are rounded at both anterior and posterior ends, the anterior end usually marked by a small indentation or groove. The crown may be evenly convex, or thickest in the middle, and slightly posterodorsally oriented. The basal plate is convex, and only slightly exposed. This denticle shape is usually found in the primary denticle band, and in the scapular area, with size ranging between 2-3 mm. (Figure 2.1.3c).

Heart-shaped denticles are broadly double-rounded anteriorly, and broadly triangular posteriorly. The crown may be flat, or evenly convex (globular appearance) and slightly posterodorsally oriented. Much of the convex basal plate is usually exposed. Enlarged (3-5 mm) heart-shaped denticles with convex surface are confined to the mid-scapular area, and smaller ones (1-2 mm) evenly distributed on the dorsal surface of the disc, including the tail. (Figure 2.1.3d).

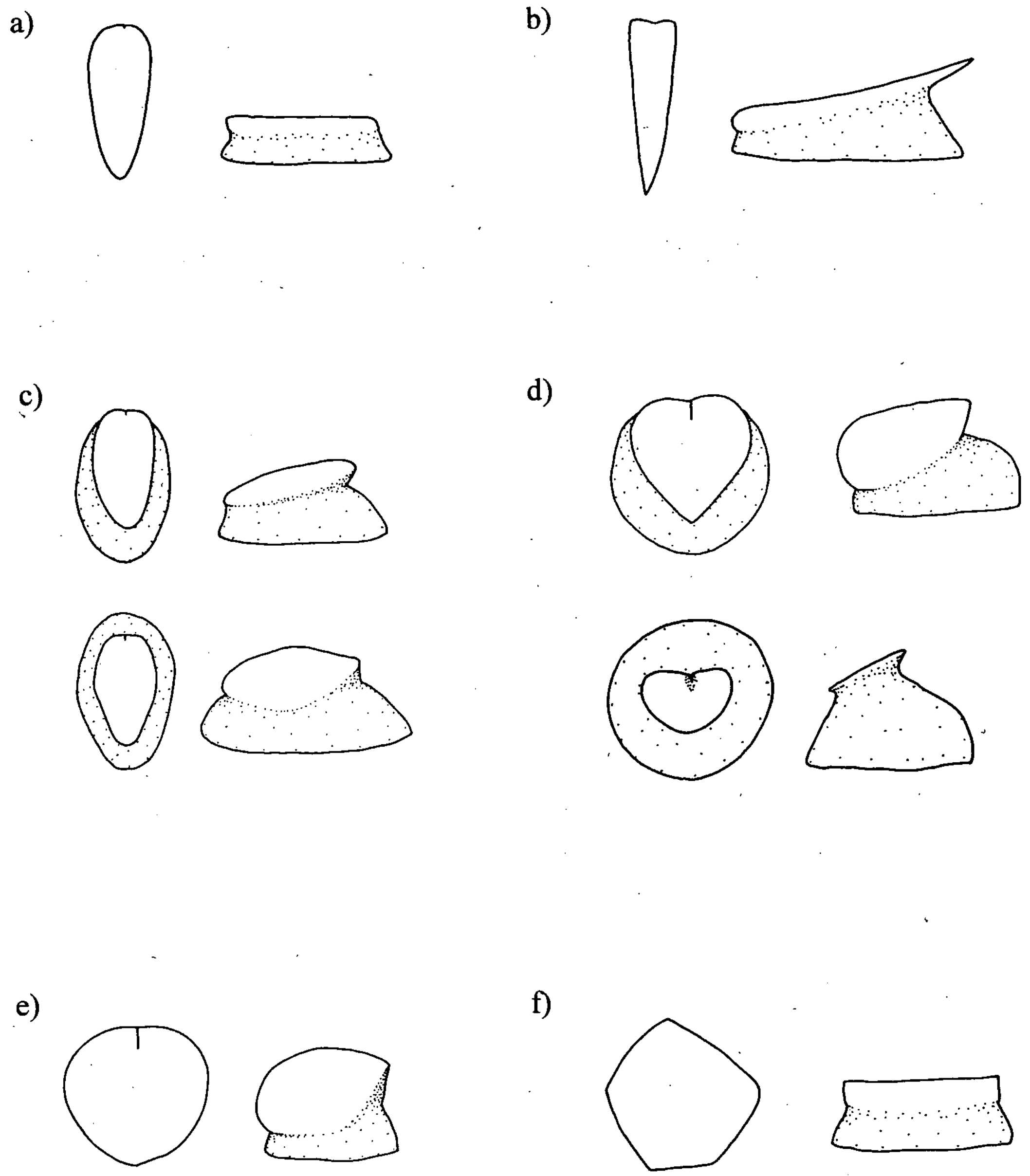


Figure 2.1.3. Denticle shapes of Indo-Pacific whip-tailed stingrays- dorsal (left) and lateral (right) views. Anterior positions are top of dorsal views and left of lateral views. a) seed, b) lanceolate, c) ovate, d) heart, e) pearl, f) irregular. Plain area indicating the crown; shaded area the basal plate. Not drawn to scale.

Pearl-shaped denticles are almost well-rounded, globular in appearance, and reduced basal plate. This denticle shape is confined to the mid-scapular area, and along the trunk above the abdominal cavity. Sizes range from 2 mm. (Figure 2.1.3e).

Irregular-shaped denticles, are small flattened interstitial denticles, occupying spaces between the larger 'more conformed shaped' denticles, as in a mosaic pattern. Therefore, these denticles do not have a set shape, but their polygonal appearance is characterized by the space they occupy. (Figure 2.1.3f).

Developmental stages of squamation

Six stages of squamation are identified in the dasyatids. These stages are described in order of ontogenetic development, and the size-range of each stage given. The features of each denticle and thorn type, i.e. shape, size, density, and loss of features as evident in earlier stages (e.g. denticles becoming smaller, blunter, falling out) are noted and discussed within the appropriate stages (Radcliffe 1917; P. Last pers. comm.). The classification of squamation is defined as follows:

Stage 0: Disc entirely smooth (naked), or with only 1-3 prominent embryological, suprascapular denticles. The embryological denticles may be uniform or variably shaped and of varying sizes. Actual size of the denticles is given in the description.

Stage 1: Development of primary median denticle band adjacent the suprascapular denticles; this band consists of a narrow band of small and enlarged denticles (usually smaller than suprascapular denticles) arranged in 1-3 rows; those in the median row are slightly larger than those on the adjacent outer-side. The band is either confined to the anterior disc or extends along mid-line on to the tail; differential denticles may appear on the tail beyond the sting during this stage or at a later stage (Stage 3).

Stage 2: Initial stage for development of discontinuous or irregular secondary denticle patch(es); one or two patches may be present; patch(es) confined to the disc (on head and near earlier structures) and may show distinctive shape for each species throughout the development of this stage; denticles smaller than embryological and primary denticles, usually well-spaced and non-imbricated.

Stage 3: Development of independent row(s) of enlarged denticles along the midline of the tail; caudal structures are usually different in shape and/or size to embryological, primary and secondary denticles.

Stage 4: Secondary denticle patches coalesced to form continuous, regular, longitudinal band on disc with extension on to the tail; denticle band shape, width and extension variable between species; denticles often decreasing in size laterally from midline, and more closely spaced than those at Stage 2.

Stage 5: Development of small tertiary denticles on disc outside secondary band; denticles usually small, different in shape to secondary denticles, often granular or more spine-like and may be aggregated or evenly distributed.

Stage 6: Development of tertiary spiny thorns (bucklers) over disc; denticles upright, pungent, larger than all other dermal structures.

In order to quantify the squamation description, a series of measurements of the nuchal denticle and denticle band is proposed. Following are the measurements, listed in alphabetical order (Figure 2.1.4):

1. Length of largest nuchal thorn (NUL): horizontal length of the largest nuchal thorn.
2. Length and width of the primary denticle band (1L, 1W).
3. Distance of anterior of primary denticle band from posterior end of spiracle (1S).
4. Width at interorbital distance (2IO): width of the secondary denticle band at the position of the interorbital width.
5. Naked snout ratio (2O): naked area from tip of snout to anterior of secondary denticle band.
6. Narrowest width between end of spiracles and scapulocoracoid (2W): the narrowest width of the secondary denticle band between the inner posterior margin of spiracle and scapulocoracoid; there is no fixed point for this measurement, readings are recorded as '0' when the two denticle patches over the fontanelle and the first synarcual are not connected.
7. Width at pectoral-fin insertion (2WP1): width of the secondary denticle band at pectoral-fin insertion.
8. Width at scapulocoracoid (2WSc): width of the secondary denticle band above the scapulocoracoid.
9. Width at distance halfway between scapulocoracoid and pectoral insertion (2WScP1): width of the secondary denticle band at distance halfway between scapulocoracoid and pectoral insertion.

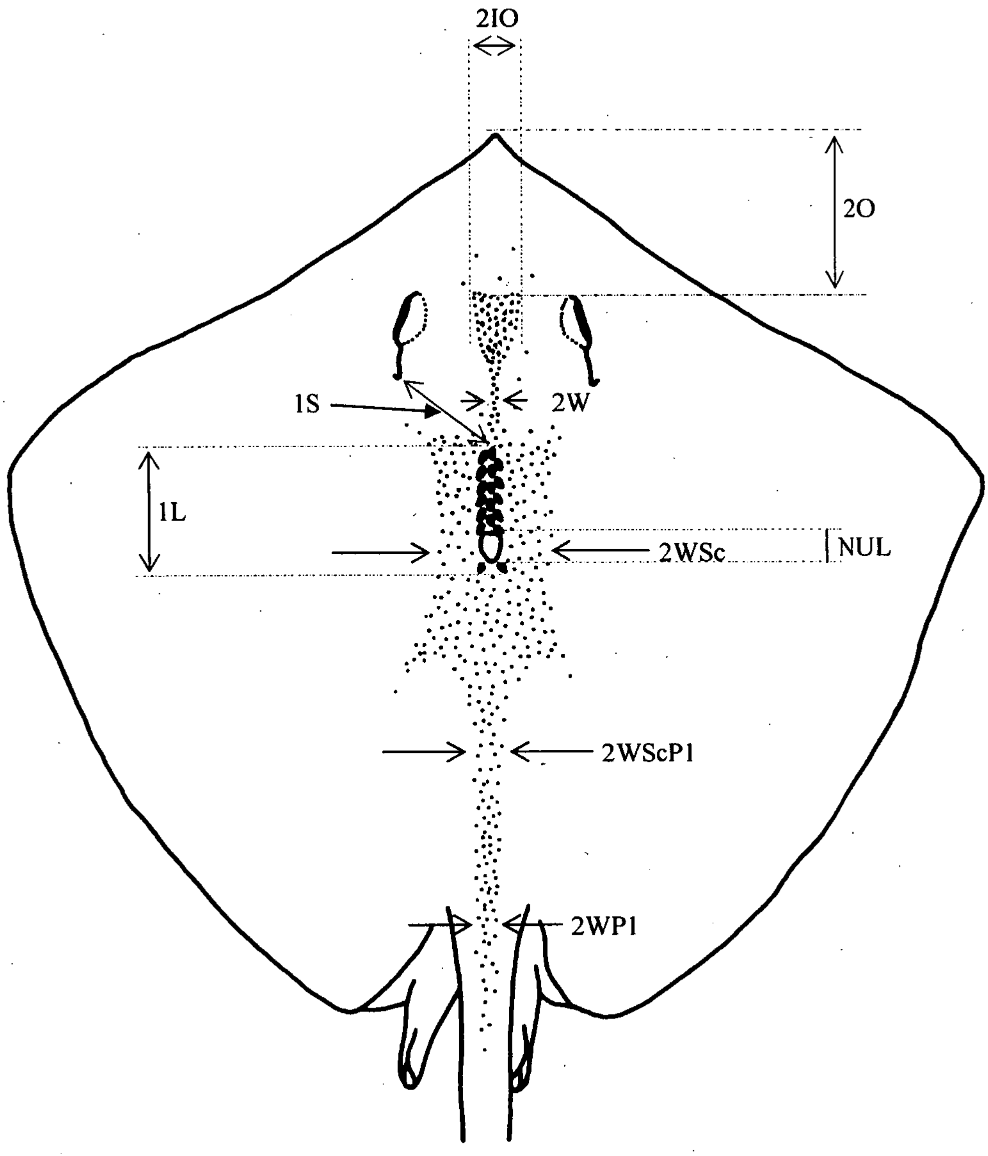


Figure 2.1.4. Denticle and denticle band measurements. NUL- length of largest nuchal denticle, 1L- primary denticle length, 1S- Distance between anterior tip of primary denticle band to posterior end of spiracle, 2IO- Width at interorbital distance, 2O- Naked area from tip of snout to anterior of secondary denticle, 2W- Narrowest width between end of spiracles and scapulocoracoid, 2WP1- Width at pectoral fin insertion, 2WSc- Width at scapulocoracoid, 2WScP1- Width at distance halfway between scapulocoracoid and pectoral insertion. See text for definitions.

2.1.2.5 Skeletal characteristics

Standard dissections for skeletal parts include the neurocranium, scapulocoracoid, pelvic girdle, and clasper. Dissection of parts from preserved specimens was made by making an incision through the skin, removing the tissues surrounding the parts, then extracting out the specified parts. The cavity created by removal of the parts was re-filled with tissue paper, and the incisions made on the surface (skin) of the specimens sewn back together. Some of the preserved claspers were stained and cleared, using methods suggested by Dingerkus and Uhler (1977), Taylor and Van Dyke (1985), and Song and Parenti (1995). In most cases, however, structures were observed without staining. Preparation of skeletal parts from fresh specimens in the field was simply made by leaving them out to rot at room temperature for 1-3 days. Excess muscle tissues were then manually removed, and the cleaned parts preserved directly into 75% ethanol. Earlier trials on the effects of formalin on these cartilaginous skeletons revealed a similar effect as that on fish otoliths (McMahon & Tash 1979), in that these cartilaginous parts become brittle within a few days of storage in unbuffered formalin. It is thought that formalin reacts negatively with the calcium content in these skeletal structures. The elasmobranch cartilage is in the form of crystallites of hydroxy-apatite, $3(Ca_3PO_4)_2Ca(OH)_2$, deposited in an organic matirx (see Kemp 1999), and the otoliths, are primarily composed of calcium carbonate, $CaCO_3$ (see McMahon & Tash 1979).

Terminology of skeletal features

Terminologies for analogous structures in sharks and rays have either confused their usage (as noted by Hulley 1972) or been rejected by others (e.g. Taniuchi & Ishihara 1990). This is especially prevalent when the study involved only external morphology without reference to the internal cartilages, particularly the claspers. In this study, the terminologies adopted were based on the accurate definition and/or widest usage in literature, and where possible, attempts were made not to discriminate analogous terminologies between sharks and rays. The terminologies used are listed in the following, in alphabetical order under the heading of each skeletal part examined. The position of each structure is also described and additional notes appended.

Neurocranium (Figure 2.1.5)

ac anterior cerebral vein foramen (Compagno & Roberts 1982; Nishida 1990); located anterodorsally to the optic nerve foramen.

antc antorbital condyle (Compagno & Roberts 1982); located on the posterolateral corner of the nasal capsule, it is where the neurocranium articulates with the antorbital cartilage.

apoc anterior preorbital canal foramen (Nishida 1990); located dorsally at the base of the preorbital process.

bp basal plate (Compagno & Roberts 1982); forms the neurocranium floor.

elf endolymphatic foramen (Nishida 1990); the anterior pair of two pairs of lymphatic foramina present on the dorsal surface of the otic region.

esaf efferent spiracular artery foramen (Nishida 1990); located posteroventrally to the base of the optic stalk.

f fontanelle (Compagno & Roberts 1982; Nishida 1990); the opening of the cerebral cavity; it is sealed by a strong membrane.

hf hyomandibular facet (Compagno & Roberts 1982; Nishida 1990); a shallow depression, generally oval shaped, lying horizontally; located on the ventrolateral corner of the otic region.

icaf internal carotid artery foramen (Compagno & Roberts 1982; Nishida 1990); located on the postero-ventral surface of the neurocranium.

ioc interorbital canal foramen (Compagno & Roberts 1982); position variable for different species, but always located anterior of the orbital fissure.

ip internasal plate (Compagno & Roberts 1982); separates both sides of the nasal capsule.

lc lateral commisure (Compagno & Roberts 1982; Compagno 1988); cartilaginous bridge lateral to the head vein on each side of the otic capsule.

nc nasal capsule (Compagno & Roberts 1982; Nishida 1990); the anterior part of the neurocranium, encasing the olfactory organs; the capsules are expanded ventrolaterally, and opens ventrally; usually with three nasal cartilages present on the margin of the opening, reinforcing the nasal flaps; the three cartilages, inner nasal cartilage, outer nasal cartilage and posterior nasal cartilage, are of variable shape, with the inner nasal cartilage fused to the neurocranium.

oc occipital condyle (Compagno & Roberts 1982); condyle for articulation with the synarcual; located on both sides of the articular surface on the posteroventral surface of the neurocranium.

of orbital fissure (Compagno & Roberts 1982; Nishida 1990; McEachran & Last 1994); a large foramen located at the junction of the orbit and otic region; this term is confusing as it is actually a foramen rather than a fissure; the usage of this term is retained due to its wide usage; a fissure above it, present in only some of the species examined, is termed pseudo-orbital fissure.

onc orbitonasal canal foramen (Compagno & Roberts 1982; Nishida 1990); located below the posterior foramen for the preorbital canal.

os optic stalk (Compagno & Roberts 1982; Nishida 1990); a shaft, extending from the lateral wall of the orbit just behind the optic nerve foramen.

plf perilymphatic foramen (Nishida 1990); the posterior pair of two pairs of lymphatic foramina present on the dorsal surface of the otic region.

pof pseudo orbital fissure (this study); a shallow fissure located beneath the postorbital process, and above the orbital fissure.

pop postorbital process (Compagno & Roberts 1982; Nishida 1990); Nishida also demonstrated that the small triangular posterior section of the supraorbital crest is part of the expanded wing-like postorbital process; the wing-like structures are located on the dorsolateral corners of the otic region.

ppoc posterior preorbital canal foramen (Nishida 1990); located dorsally at the junction of the nasal capsule and orbit, and is occupied by a branch of the facial nerve.

prop preorbital process (Compagno & Roberts 1982; Nishida 1990); a compact, laterally projecting structure located above the antorbital condyle.

soc supraorbital crest (Nishida 1990); a ledge-like structure above the orbit, originating from the base of the preorbital process, and extending posteriorly to end at the base of the postorbital process.

sr sphenopterotic ridge (Compagno & Roberts 1982); ridge bordering the dorsolateral surface on the posterior of the otic region.

II optic nerve foramen (Compagno & Roberts 1982; Nishida 1990); the largest foramen located centrally on the orbital wall just anterior to the base of the optic stalk.

III oculomotor nerve foramen (Compagno & Roberts 1982; Nishida 1990); located just dorsally to the base of the optic stalk.

IV trochlear nerve foramen (Compagno & Roberts 1982; Nishida 1990); located posterodorsally to the optic nerve foramen; variable number for different species.

VII hyomandibular branch of facial nerve foramen (Nishida 1990); located behind/under the lateral commisure.

IX glossopharyngeal nerve foramen (Compagno & Roberts 1982; Nishida 1990); located on the posterior surface of the neurocranium, dorsolaterally to the occipital condyle.

X vagus nerve foramen (Nishida 1990); located just laterally to the foramen magnum (spinal cord foramen).

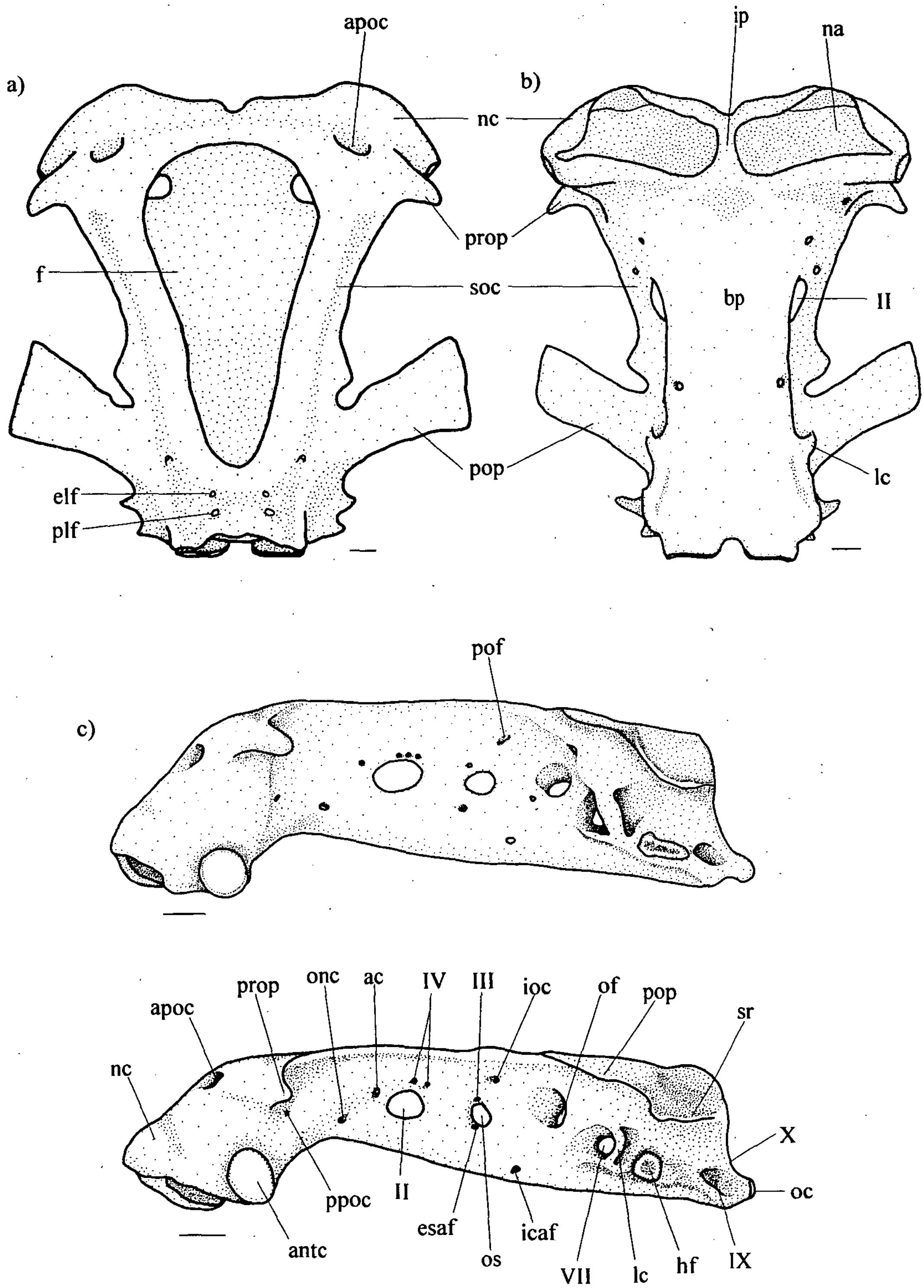


Figure 2.1.5. Outline illustration of the neurocranium of a representative dasyatid. a) dorsal view; b) ventral view; c) lateral view. See text for definitions. Bars indicate 10 mm.

Scapulocoracoid (Figure 2.1.6)

adf anterodorsal fenestra (Compagno & Roberts 1982; Nishida 1990); inside wall connecting it to the fenestra of the scapular process above, shaped like a twisted 'S'.

ar anterior ridge (Compagno & Roberts 1982); a plate-like structure separating the anterodorsal and anteroventral fenestra; the structure may be level or sloping outwards in lateral view.

avf anteroventral fenestra (Compagno & Roberts 1982; Nishida 1990); behind it is the coracoid bar that joins both sides of the scapular.

msc mesocondyle (Compagno & Roberts 1982; Nishida 1990); located along the horizontal axis of the scapulocoracoid, it is where the scapulocoracoid connects with the mesopterygium.

mtc metacondyle (Compagno & Roberts 1982; Nishida 1990); located on the posterior end of the horizontal axis of the scapulocoracoid, it is where the scapulocoracoid connects with the metapterygium.

pdf postdorsal fenestra (Compagno & Roberts 1982; Nishida 1990);

prc procondyle (Compagno & Roberts 1982; Nishida 1990); located on the anterior end of the horizontal axis of the scapulocoracoid, it is where the scapulocoracoid connects with the propterygium.

pvf postventral fenestra (Nishida 1990); variable aperture size and number.

spf fenestra of the scapular process (Lovejoy 1996); variable aperture size, number and depth.

Pelvic girdle (Figure 2.1.7)

ilp iliac process (Compagno & Roberts 1982; Nishida 1990); a thin posterodorsally projected process, located on each lateral extremity of the pelvic girdle.

isp ischial process (Compagno & Roberts 1982); a small, posteriorly directed projection, located at an angle opposite the lateral prepelvic process on the inner margin of the pelvic girdle.

lpp lateral prepelvic process (Nishida 1990); a short, stout, anterolaterally directed prepelvic process on the anterolateral corner of the pelvic girdle.

obf obturator foramina (Compagno & Roberts 1982; Nishida 1990); located on the thickened lateral extremes of the pelvic girdle; variable in number.

pi puboischiadic bar (Nishida 1990); the 'main frame' of the pelvic girdle; anteriorly arched, more or less depressed in cross section; thickened at its lateral extremes where the obturator foramina are located.

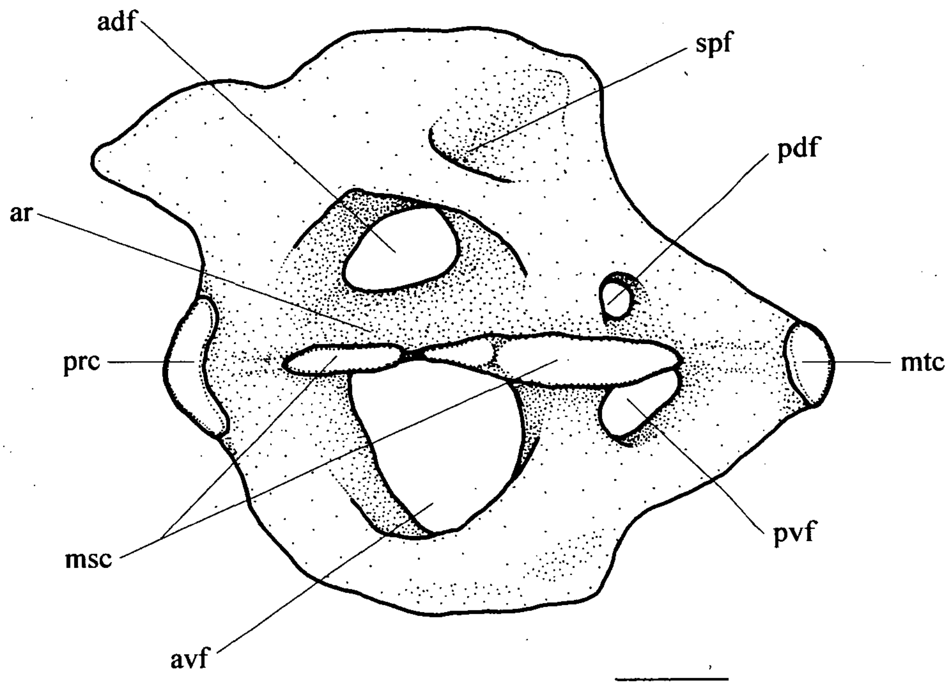


Figure 2.1.6. Outline illustration of the left scapulocoracoid of a representative dasyatid. Lateral view. See text for definitions. Bar 10 mm.

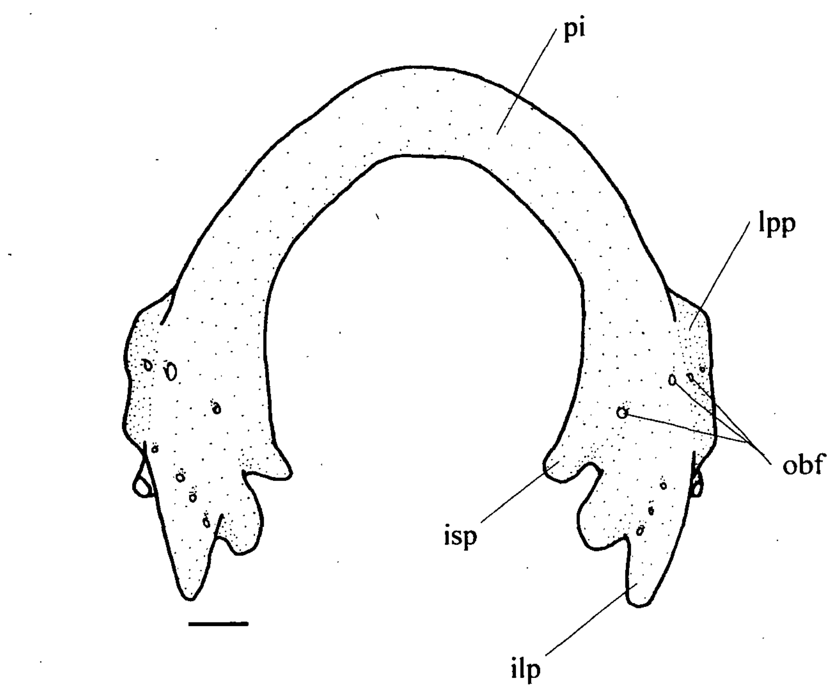


Figure 2.1.7. Outline illustration of the pelvic girdle of a representative dasyatid. Dorsal view. See text for definitions. Bar 10 mm.

Clasper (Figure 2.1.8)

External morphology of intact clasper

apo apopyle (Leigh-Sharpe 1920; Stehmann 1970; Compagno & Roberts 1982; Taniuchi & Ishihara 1990); anterior proximal opening of the clasper, in the region of the opening of the secretion passage of the clasper gland; it is connected to the hypopyle by an open posteriorly curved clasper groove.

cgr clasper groove (Compagno & Roberts 1982; Taniuchi & Ishihara 1990); the tube-like groove along anteroposterior on the dorsomedial surface of the clasper.

hyp hypopyle (Leigh-Sharpe 1920); opening of the clasper groove in the terminal section; the hypopyle in whip-tailed stingrays is without any structures inside it (in skates, a structure called rhipidion is present inside the hypopyle) (Compagno & Roberts 1982; Taniuchi & Ishihara 1990; Nishida 1990).

psp pseudopera (Compagno & Roberts 1982); the terminal opening below the hypopyle.

pss pseudosiphon (Hulley 1972; Compagno & Roberts 1982); a cavity situated on the outer surface of the dorsal lobe of the clasper glands; it has an oval aperture, the long axis of which is orientated in the longitudinal axis of the organ.

Clasper skeleton (mixopterygium)

axc axial cartilage (Compagno & Roberts 1982; Taniuchi & Ishihara 1990); forms the basic foundation of the clasper, is a bar-like cartilage terminating at the distal end of the clasper; from its proximal end to the level of the commencement of the glands, the axial is nearly completely enclosed by dorsal and ventral marginal cartilages, so as to form a tube (clasper groove) on the outer lateral surface of the axial; usually much less calcified than the other cartilages.

B basal segment (Compagno & Roberts 1982); the basal segment articulates the pelvic basipterygium (=pelvic metapterygium) and the axial cartilage; usually two basal segments are present, but a third one may be present in some species; the first, second and third basal segments are labeled accordingly, i.e. B1, B2, and B3.

β beta cartilage (Compagno & Roberts 1982; Taniuchi & Ishihara 1990); a long depressed cartilage flange originating anteriorly over, or from (this study) the basal segments and merging posteriorly with dorsal marginal cartilage, or with the axial cartilage (this study).

cgl clasper glands (Leigh-Sharpe 1920); compact, large gland with muscular walls, bean-shaped; extending on the ventral side over the entire length of the posterior lobe of the ventral (pelvic) fin directly beneath the integument, drawn as a protuberance; dorsally lying immediately adjacent to the fin rays.

mcd dorsal marginal cartilage (Compagno & Roberts 1982; Nishida 1990); a somewhat proximally broadly pointed, distally expanded cartilage; it tightly attaches to the axial cartilage and running along its outer lateral margin.

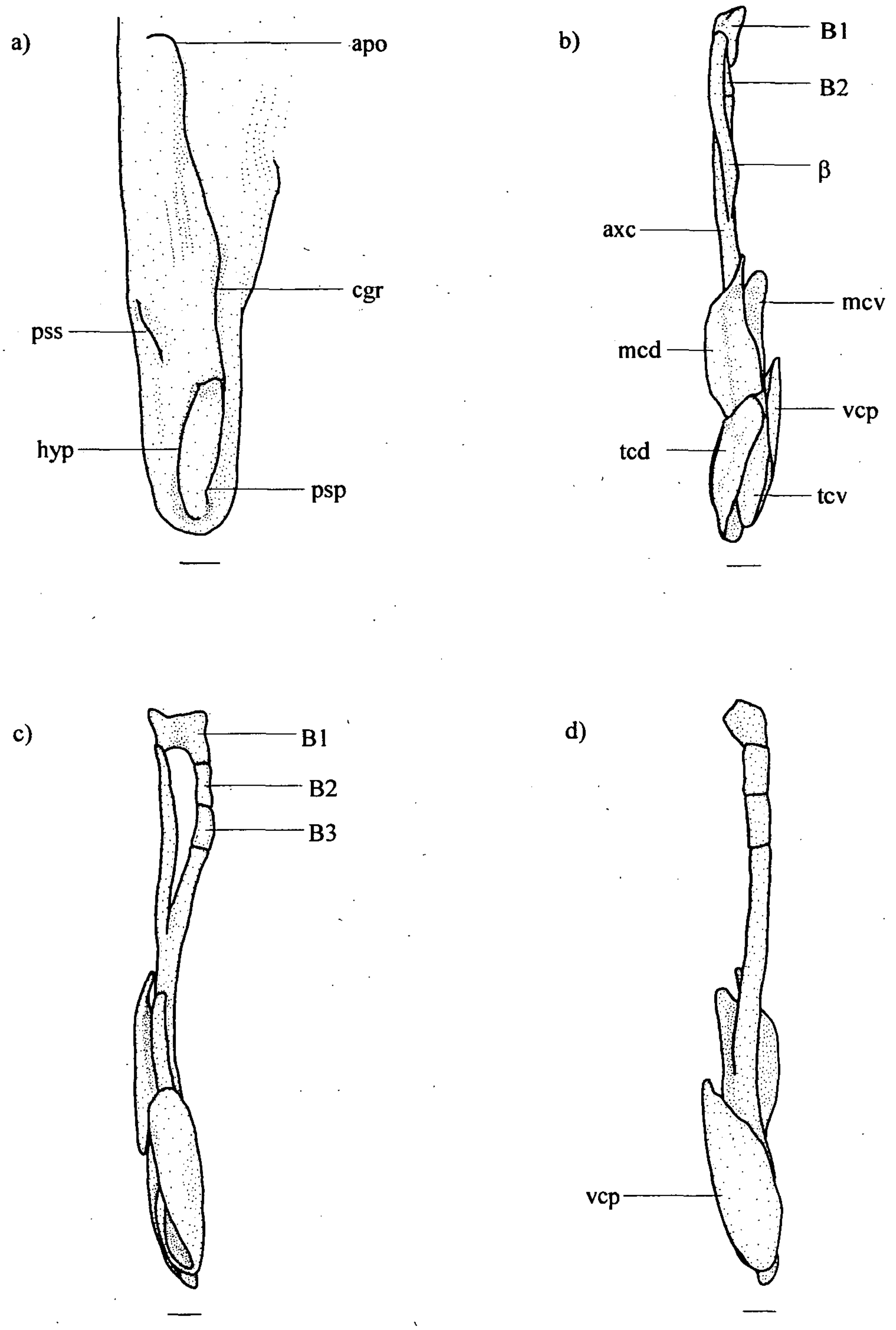


Figure 2.1.8. Outline illustration of the right clasper of a representative dasyatid. a) dorsal view of intact clasper; b-d) dorsal, lateral and ventral views of dissected clasper. See text for definitions. Bars 10 mm.

mcv ventral marginal cartilage (Compagno & Roberts 1982); a laterally expanded plate on the axial cartilage, whose outer lateral edge forms the ventral margin of the clasper groove; it extends further along the length of the clasper than the dorsal marginal cartilage, and distally is usually expanded and ventrally convex.

tcd dorsal terminal cartilage (Compagno & Roberts 1982; Nishida 1990); a broad, medially grooved, wedge-shaped cartilage whose anterior base articulates with the posterior edge of the dorsal marginal; its posterior end narrow, and medial edge attached to the axial cartilage; this cartilage also forms the wall of the hypopyle.

tcv ventral terminal cartilage (Compagno & Roberts 1982; Nishida 1990); located below the dorsal marginal cartilage, it is a broad lateral flange forming the roof of the pseudopera and a recurved posterolateral tip forming a partial floor under it.

vcp ventral covering piece (Compagno & Roberts 1982; Nishida 1990); a shield-like cartilage, covering the ventral surface of the clasper.

2.1.2.6 Ventral lateral lines

Observations of the pattern of the ventral lateral line canals were made on preserved post-embryonic specimens (Melouk 1959). The subepidermal position of these canals, and the pale colour of the ventral skin of most species makes it possible to observe the patterns directly through the skin. Most often, however, it was necessary to dissect out the skin on the ventral surface, and this was done using a scalpel blade (N. Lovejoy, pers. comm.). The patterns were then traced onto a transparent plastic sheet. Terminologies follow Lovejoy (1996) and McEachran *et al.* (1996) (see also Chapter 3, Figure 3.2.6).

2.1.3 Species descriptions

Species descriptions are presented based on a hypothesized phylogenetic relationship using morphological and molecular data sets. They cover all recognized and valid species, followed by new species, listed as *Himantura* sp. A, *Himantura* sp. B etc. However, species from different localities are treated as one although population differences may exist. Doubtful species are placed as *incertae cedis*. Nomenclatural procedures follow the fourth edition of the International Code of Zoological Nomenclature (ICZN 1999), hereafter referred to as the 'Code'. Therefore, new species identified herein will be described in appropriate journals.

For each species description, the holotype traits are given first, followed by the range variability in the typical specimen series. All other non-type specimens examined are listed at the end of the species description. Synonymies include the original description, and the first usage of new nomenclatural combinations, emendations, misspellings, and misidentifications. However, a complete synonymy is given only for lesser known species. Reference to a taxonomic name other than the original description is presented by placing a colon after the taxon name. This is followed with a one-paragraph account of diagnostic characteristics of the species.

The species description is given in a six sub-heading format, describing the external morphology of the disc, features of the head (snout, eyes, oronasal, and gill openings), meristic counts, squamation, colouration, and skeletal morphology. All descriptions are supported with images of type(s) and/or representatives, and a table listing the proportional measurements, counts and meristic values. Additional information include known size, etymology, common name, and known distribution. A discussion on closely-related species is given in detail under the comparisons section, and other pertinent information under the remarks section.

The morphometric data for each species are presented as a percentage (%) of disc width, separately listing measurements for types and non-types. Holotype and other types are further separated, and data for all specimens other than the holotype are presented in ranges, unless only one representative of the species was examined. The practice of expressing measurements against a standard length, in this case, 'as a percent of disc width' to correct for differences in specimen sizes between samples, is widely applied in taxonomic studies (e.g. Cailliet *et al.* 1986; Last & Stevens 1994). Furthermore, the extreme morphometric variation between different maturity stages, and the small sample number meant that use of statistical techniques for data analysis was limited, as demonstrated by Fechhelm and McEachran (1984), Yearsley (1988), and Miyake (1988).

On the other hand, a method using proportional data to detect possible additional characteristic data, proved useful, particularly between members of a species complex. The method, suggested by P. Last (pers. comm.), uses a simple technique, whereby, the proportional data of the taxa in question are arranged in columns to produce a new data set. Pairs of 'high' and 'low' range value(s) in the new data set were then determined by eye. The values of such data (if they exist), are emphasized by dividing the high and low value of a taxon or a group, and comparing it with a matching pair from another taxon or taxa.

Meristic data given are range values for both the left and right side. Anatomical data were compared and described to provide information on species description which otherwise cannot be described by morphometric techniques.

2.1.4 Photography and line illustration

Photographs of whole specimens were taken in the field, and indoors, using a 35 mm film for colour slides and prints (usually of *Kodak* 200 or 400 speed). Photographs of skeletal parts were all taken indoors on a black and white print film (*Kodak T400*). The parts were placed on a light-box for background lighting, and light bulbs mounted on either side of the object for foreground lighting and to create a three dimensional view of the parts. All images were scanned, and digitally enhanced for the final presentation (Day 1995). Line illustrations of skeletal parts were initially produced by tracing by hand enlarged images of photo prints. The images for tracing were enlarged up to twice the size of the final output, to maintain the fine lines of the outline illustrations after scanning and resizing. All final image layouts were created in Adobe Photoshop and Microsoft PowerPoint.

All images are scaled down to the same size, and where possible presented along the same positional view. However, images taken other than in a fixed setting during special photo sessions were not always perfect. These were taken from different angles, other than from dorsal vertical, thus presenting a parallax problem. In these cases, little could be done to improve their presentation, and thus are presented as they were taken. It is noted though, that for such images the emphasis is on the disc colour pattern rather than disc shape.

Images were also digitally enhanced for the sake of uniformity and perfection. For example, the right part of a skeletal structure might have been dissected, but it is 'horizontally flipped' during image manipulation so that it appears as the left part for the final presentation. As for disc shapes, pins and folded edges were masked to produce a smooth disc edge. However, it should be noted that such a step was applied only to non-type materials, with images of all type materials presented in their exact condition.

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CHAPTER 3

3.0 MORPHOLOGICAL PHYLOGENY

The Family Dasyatidae is the largest and one of the most diversified ray groups of the Order Myliobatiformes. The family includes endemic as well as circumglobal species from tropical and sub-tropical regions, with an estimate of at least 60 species, which are classified into at least 5 genera (Compagno 1999a, b; Last & Compagno 1999).

Recent morphological (Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a) and molecular (Lovejoy *et al.* 1998; Sezaki *et al.* 1999; Chen *in press*) based systematic studies have highlighted the taxonomic confusion surrounding dasyatids, in which members within the genera *Dasyatis* and *Himantura* are shown to be poly- and paraphyletic. Such confusion has long been echoed by authors working on lower- (Last 1979, 1987; Compagno & Roberts 1982) and higher- (Maisey 1984) level systematics. Nevertheless, on a higher level, batoids (all ray fishes, from the shark-like guitarfishes to discoid mantas) are monophyletic (Compagno 1973, 1977, 1999a, b; Nishida 1990; McEachran *et al.* 1996).

The compositional stability of the family Dasyatidae is systematically weak, and there is clearly a need for taxonomic revision of its members. As to the present time (this study), the generic classification within Dasyatidae is largely without phylogenetic basis, but instead based primarily on general external similarity, especially on tail morphology. The genera of the family Dasyatidae as currently recognized are *Dasyatis*, *Himantura*, *Pastinachus*, *Pteroplatytrygon*, *Taeniura* and *Urogymnus* (Compagno 1999b; Last & Compagno 1999).

Historically, dasyatids have always been closely associated with potamotrygonids (river rays in tropical and sub-tropical South America) because of the general similarity of the disc shape and the whip-like tail (Garman 1913; Bigelow & Schroeder 1953). However, many studies have demonstrated the uniqueness of the South American freshwater stingray from marine stingrays, in terms of morpho-anatomical and physiological characteristics (reviewed by Rosa 1985). Furthermore, Lovejoy (1996) in an effort to infer the historical relationship of the potamotrygonids with the marine stingrays, has been able to show that two amphi-American stingrays currently designated under the genus *Himantura*, have a closer affinity to the potamotrygonids, than to the Indo-West Pacific *Himantura*.

Based on the results of his analysis, Lovejoy (1996) further suggested that the Indo-Pacific *Himantura* has a closer relationship to *Dasyatis*. In a separate study on the phylogenetic interrelationship of batoids, McEachran *et al.* (1996) followed Lovejoy in lumping Indo-Pacific *Himantura* with *Dasyatis*. Consequently, in the latter study, no Indo-Pacific *Himantura* species were examined, and as in Lovejoy, only amphi-American representatives of *Dasyatis* were examined, including one cosmopolitan species *D. violacea*.

As with *Himantura*, *Dasyatis* is represented in both the Indo-Pacific and amphi-American regions. Additionally, *Dasyatis* include all known freshwater whip-tailed stingrays from the African continent (Compagno & Roberts 1984; Compagno & Cook 1995; Compagno 1999b). The phylogenetic analysis within myliobatidoids (all discoid rays, excluding skates and other intermediate forms i.e. electric rays), in which Nishida (1990) determined to be a monophyletic group, did not detect any zoogeographical (i.e. either Atlantic or Pacific Ocean) affinity, particularly within *Dasyatis*. Instead, the potamotrygonids (*Potamotrygon*) and three other genera (*Taeniura*, *Dasyatis*, and *Himantura*) were placed under Dasyatidae. Nishida's assessments also supported a monophyletic *Dasyatis* and *Himantura*.

Most recently, Rosenberger (2001a) tested Lovejoy's (1996) hypothesis of the paraphyletic interrelationship within *Dasyatis*. Using a subset of dasyatid species, she attempted to specifically test geographical affinities of members based on cladistic analysis. This study not only confirmed Lovejoy's hypothesis, but revealed several sister relationships within the genus. The result of the analysis further supported Indo-Pacific *Himantura* as being nested within *Dasyatis*, albeit supported by a set of different characters from that used by Lovejoy and that there was no clear pattern regarding the zoogeographical affinities, especially among the sister pair relationships within *Dasyatis*.

The generic status of *Pteroplatytrygon* and its sole member *P. violacea* (originally described as a *Dasyatis*) has always been a source of debate since it was formed by Fowler (1910). While Fowler suggested the unique disc shape (disc wider than long, and anterior margin broadly convex) as the only diagnostic feature of this monotypic genus, others have found more characters unique to the species to support the genus. Some of these characters include structure of dermal denticles and dentition, as reviewed by H. Mollet (pers. comm., 2001). Mollet himself has a personal interest in the systematic classification of *P. violacea* from his involvement in studies relating to the biology of this pelagic stingray (e.g. Mollet *et al.* 1996). More recently, based on her studies regarding swimming behaviour in stingrays, Rosenberger (2001b) found that the swimming 'strategy' of this species is unique among other *Dasyatis*. However, Rosenberger, as others (Nishida 1990; Lovejoy 1996; McEachran *et al.* 1996), treated the species as a *Dasyatis* in their phylogenetic analyses. The results of these studies show the species as nested among other *Dasyatis*.

As for another recognized genus *Taeniura*, the phylogenetic analysis by Nishida (1990) resulted in it being in a polytomy clade including *Potamotrygon* and *Dasyatis*, with an unresolved relationship between two members (*T. lymma* and *T. meyeni*) of the genus. Lovejoy (1996) however, revealed its polyphyletic status, suggesting *T. lymma*, a widely distributed species in the Indo-West Pacific (Last & Stevens 1994), as a link between the amphi-American *Himantura* + potamotrygonids and dasyatid (*Dasyatis* + Indo-Pacific *Himantura*) + gymnurid + pelagic myliobatiforms. On the other hand, based on the examination of three Galapagos Island and Somalian specimens, it has been suggested that *T. meyeni* is more closely related to *Dasyatis* and the Indo-Pacific *Himantura* (Lovejoy 1996). McEachran *et al.*'s (1996) finding regarding the relationship of *T. lymma* was identical with Lovejoy, while Rosenberger's (2001a) analysis indicated *T. lymma* as basal to all *Dasyatis* including *Pastinachus*.

The monotypic genus *Pastinachus*, as with *Pteroplatytrygon*, has also been constantly disputed among systematists. Nishida (1990) treated the species *Pastinachus sephen* as *Dasyatis*, and did not find it to deviate from this treatment as a result of his study. Rosenberger (2001a) however, considered the species under the genus *Pastinachus* following Compagno (1999b). Rosenberger conceded that she did not find any unique character apart from it having an extremely deep ventral tail fin fold. However, Rosenberger suggested further analyses to warrant a name change for the monotypic genus *Pastinachus*. On the other hand, based on several on-going studies by Compagno, and Last and Manjaji, a second and even third species may be present, and that several characteristics may hold up to support this genus. These include morpho-anatomical characteristics such as squamation, dentition, skeletal characteristics and clasper morphology. According to Roberts (1998), the taxonomic status of this species is tentative, and therefore requires further revision.

A sixth recognized genus, *Urogymnus*, remains the only genus within Dasyatidae whose members have yet to be phylogenetically assessed. Compagno (1999b) listed two species, *U. asperrimus* and *U. ukpam*. The first species, whose type was found in the Indo-Pacific (Last & Stevens 1994; Fowler *et al.* 1999), is extremely rare. The second species, which is a freshwater species from West Africa, was originally considered as a *Dasyatis* based on the presence of a ventral tail skin fold (Compagno & Roberts 1984). According to Last and Stevens (1994), there may be several more undescribed species of this genus.

The non-monophyletic composition of the family is shown from the results of studies on the interrelationship within members of Dasyatidae, albeit with varying findings on the relationships. In particular, is the relationship between *Dasyatis* and *Himantura*. Currently, only one character is recognized in distinguishing the two (i.e. the presence of tail skin fold would render a species as a *Dasyatis*, and lack of it as *Himantura*). The character is also conveniently used as a basis to further distinguish other genera of the family (Last & Stevens 1994). As mentioned previously (see Taxonomic Revision, Chapter 2), results of phylogenetic systematic analyses of rays (Nishida 1990; Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a) have demonstrated that the tail skin fold character alone did not form a basis for resolving the interrelationship between *Himantura* and *Dasyatis*.

McEachran *et al.* (1996) attributed the differences in resolution between two competing hypotheses of batoid relationship (specifically between Nishida [1990] and Lovejoy [1996]), to differences in taxa analyzed, characters used, and character coding. Therefore, combining of the Indo-Pacific *Himantura* and *Dasyatis* together (Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a), remain ambiguous.

The aim of this study is to test the monophyly of Indo-Pacific *Himantura*, based on the taxonomic revision carried out in Chapter 2. The Indo-Pacific *Himantura*, which includes all Indo-Pacific whip-tailed stingrays lacking a tail skin fold, was selected as the main group of interest within the Family Dasyatidae as a result of a preliminary survey on species diversity in the south-east Asian sub-region (Fowler *et al.* 1999; Fowler *et al.* 2002). Concurrently, a separate molecular-based phylogenetic study was carried out (Chapter 4) to independently test the monophyly of the Indo-Pacific *Himantura*. The results of these analyses will be used to delimit the taxonomic placement of the OTUs in a systematic revision of the genus (Chapter 5).

3.1 MATERIALS AND METHODS

3.1.1 Materials

Materials examined are listed in Appendix 3.1.1. These include 21 species of Indo-Pacific whip-tailed stingrays tentatively designated as *Himantura*, based on the synapomorphy of 'tail fold absent or rudimentary', and 8 non-*Himantura* Indo-Pacific stingray species, i.e. 6 *Dasyatis* species and 2 *Pastinachus* species, as the ingroup. Changes to nomenclature and names used in this chapter and in Chapter 4 relate to those defined in Chapter 5.

The Indo-Pacific *Himantura* species represent all recognized Indo-Pacific *Himantura* based on the taxonomic revision of this genus (this study), i.e. *H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga,* including 7 new species discovered in this study, i.e. *H.* sp. A, *H.* sp. B, *H.* sp. C, *H.* sp. D, *H.* sp. E, *H.* sp. F, *H.* sp. G, but excluding several tentative morphs, pending additional specimens.

The outgroup taxa include several different groups, i.e. the giant shovelnose ray *Rhinobatos typus*, the giant stingaree *Plesiobatis daviesi*, and two amphi-American *Himantura* stingrays, *H. pacifica* and *H. schmardae*.

Data for synapomorphic characters were also gleaned from the literature (Garman 1913; Chu & Wen 1979; Compagno & Roberts 1982; Capape 1983; Roberts & Karnasuta 1987; Nishida & Nakaya 1988a; Nishida 1990; Ishihara *et al.* 1993), particularly where materials were lacking, for example clasper structure of mature males.

3.1.2 Methods

3.1.2.1 Ingroup and outgroup selection

The ingroup taxa, other than the Indo-Pacific *Himantura*, were selected on the account of their occurrence within the same Indo-Pacific region. Outgroups were chosen based on phylogenetic systematic studies of batoids by Yearsley (1988), Nishida (1990), Lovejoy (1996), McEachran *et al.* (1996), and Rosenberger (2001a). In this study, *H. pacifica* and *H. schmardae* are considered as the primary outgroup taxa, and *R. typus* and *P. daviesi* as the more distant secondary outgroups following Lovejoy (1996) and McEachran *et al.* (1996). The ingroup stingrays and the primary outgroup taxa are supported as a monophyletic taxon to the exclusion of the more distant outgroups (Nishida 1990; McEachran *et al.* 1996).

3.1.2.2 Character polarity

Phylogenetic relationships were resolved using cladistic parsimony methods. Apparently however, the interpretation of 'parsimony methods' appears contentious, particularly regarding determination of the polarity of character states. Kitching *et al.* (1998) pointed out that such a notion might stem from the Hennigian argumentation (Hennig 1950, 1966 *in* Kitching *et al.* 1998), which requires *a priori* polarization of characters prior to cladogram construction. As the theory of cladistics advanced to the level of the current knowledge, they noted that the prerequisite need of *a priori* determination of character polarity has now become less significant.

Many workers are committed to the rule of parsimony advocated by Maddison *et al.* (1984). This method gives an emphasis on *a priori* resolution of outgroup relationships, with an assumption of the monophyly of both ingroup and outgroup taxa, primarily for character polarization. Other workers have shown that application of this method places unnecessary topological constraints in the analysis of the ingroup (e.g. Kitching *et al.* 1998).

Furthermore, Nixon and Carpenter (1993) stressed that arguments focusing on the superiority of the outgroup criterion for determining character polarity (see references therein) is irrelevant. They demonstrated that outgroup comparison provides a method for rooting cladograms, and the polarity of characters determined from the resulting cladogram. They also regarded all criteria as specific applications of cladistic parsimony, whose relative success is to be judged in that general framework.

In particular, the ontogenetic criterion is one most frequently employed in cladistic parsimony. This criterion is a direct method of estimating the polarity of characters. The subjectivity concerning the interpretation of a general character as the more primitive character is overcome by restricting the definition of the ontogenetic criterion to 'strict temporal precedence', so that the more general state is that which occurs first in ontogeny (Kitching *et al.* 1998). Restricting the definition of ontogenetic criterion also distinguishes it from the criterion of ingroup commonality, that criterion that assumes *a priori* character polarization (Kitching *et al.* 1998).

Of the numerous methods employing the various criteria available for determining character polarity (see Kitching *et al.* 1998 for appraisal), and other than the two detailed above, 'simultaneous, unconstrained analysis' (Nixon & Carpenter 1993) was adopted in this study. Kitching *et al.* elaborated this 'methodological phrase' as *simultaneous* because both the outgroup and ingroup taxa are analysed together, *unconstrained* because the outgroup relationships are unspecified prior to analysis.

When using this technique, the *a priori* determination of character polarity is not required; instead it is derived from the resulting cladogram. As noted by Kitching *et al.*, most computer algorithms used to estimate most parsimonious cladograms actually generate unrooted (hence unpolarized) networks. The software used in this study PAUP* (Swofford 2000) falls into this category. Thus, monophyly of the ingroup could be tested without being masked by the assumption of *a priori* character polarity.

3.1.2.3 Selection of characters and character states

McEachran *et al.* (1996) argued that the disparity in findings of batoid interrelationships was probably due to both the uniqueness of the taxa involved and to differences in the characters utilized. Thus, for this study, the character matrices of Nishida (1990), Lovejoy (1996), McEachran *et al.* (1996) and Rosenberger (2001a) were examined in detail, and the characters used by these researchers adopted when deemed appropriate, so as to minimize differences in characters utilized.

Characters surveyed for their phylogenetic significance include external and internal morphologies, and biological and physiological features. Assessment follows their topographic sequence along the anterior-posterior body axis from dorsal to ventral surfaces, and from external to internal. Presentation of the survey results also follows the same sequence. In almost all cases, observations based on literature sources were verified with independent observations. The extent of intraspecific variation especially in more cryptic species, were also investigated by examining more than one specimen where possible.

Continuous quantitative characters, e.g. morphometric and meristic data, and characters that are ambiguous or vague were excluded from analyses. Following Carpenter (1988) and Kitching *et al.* (1998), autapomorphic (uninformative) characters were also excluded from the analyses as they inflate consistency indices.

3.1.2.4 Phylogenetic analyses

The character matrix (Appendices 3.2.1, 3.2.2) was analyzed using the heuristic search option of parsimony method in PAUP* 4.0b8 (Swofford 2000). The heuristic search option was used because of the large number of taxa involved in the analysis, i.e. 31 taxa including two primary outgroups. Starting points (trees) were obtained by tree bisection-reconnection (TBR) branch swapping, using random stepwise addition, and holding 5 trees at each step. Initial branch swapping in each replicate was constrained by limiting the number of trees saved to 200, and their score greater than or equal to 100. The initial number of replications used for random stepwise addition was 100, and repeated using one value less than the best score (shortest length) generated from the initial search. The consensus tree was evaluated by means of bootstrapping (Felsenstein 1985), and bootstrap resampling repeated 2000 times (Hedges 1992). The data were run unordered to reduce subjectivity of the analysis, and were respectively coded as '?' for unknown state/ missing data, and as '&' or '$' for polymorphic states.

3.2 RESULTS

3.2.1 Comparative morphology and character analysis

3.2.1.1 External morphology

Disc (Figure 3.2.1)

The utility of the disc shape as a basis for grouping species was first used by Compagno and Roberts (1982) in their revision of the genus *Himantura*. The homology of the disc is well established based on higher systematic studies on the dichotomy of sharks and rays (e.g. Compagno 1973, 1977). In this study, attributes of the disc, i.e. snout, lateral apices and disc margins are considered as separate characters. Character state coding for these characters follows a modification of Rosenberger's (2001a: character 2) method. For example, the snout apex may be pointed, but not necessarily curved (*H. chaophraya*, Figure 3.2.1d).

An ontogenetic transformation of the disc shape, i.e. from one with an angular pectoral-fin apex to one with a broad apex (*H. pastinacoides, H. uarnak*), or from one with an acutely angular to one with a bluntly angular pectoral-fin apex (*H. toshi*), was observed. Such transformations however, are very gradual, and more readily observed when the smallest and largest individual of the same species are compared side by side. Nevertheless, in the majority of species, ontogenetic transformation of the disc shape was not observed, and thus angularity of the pectoral-fin apex was included in character matrix.

1. *Snout apex* (modified from Rosenberger 2001a: character 2). — Snout angular, coded as state 0 (Figure 3.2.1a-c) (*H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-G, *Dasyatis acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. zugei, Pastinachus sephen, P.* sp., *H. pacifica*); snout not angular coded as state 1 (Figure 3.2.1d,e) (*H. chaophraya, D. violacea, H. schmardae*).

2. *Apices of pectoral-fins.* —Acutely angular, coded as state 0 (Figure 3.2.1c) (*D. kuhlii, D. leylandii, D. violacea*); moderately angular, coded as state 1 (Figure 3.2.1a) (*H. fai, H. gerrardi, H. jenkinsii, H. uarnacoides, H. undulata, H.* sp. A-D, *D. acutirostra, D. laosensis, D. zugei, P. sephen, P.* sp.); not angular, or obtusely angular, coded as state 2 (Figure 3.2.1b,d,e) (*H. chaophraya, H. granulata, H. imbricata, H. oxyrhyncha, H. signifer, H. walga, H.* sp. E-G, *H. pacifica, H. schmardae*). The states in *H. pastinacoides, H. toshi,* and *H. uarnak* were coded as polymorphic because of ontogenetic differentiation.

3. *Free rear tips of pectoral-fins.* — Angular, coded as state 0 (Figure 3.2.1c) (*D. kuhlii, D. violacea*); rounded, coded as state 1 (Figure 3.2.1a,b,d,e) (all Indo-Pacific *Himantura, D. acutirostra, D. laosensis, D. leylandii, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

Orbit-spiracle (Figure 3.2.2)

The outline of the eyeballs is marked by a shallow groove around it, and immediately behind the eyeballs are the spiracles. The demarcation of the two is indicated by a slight indentation anterior to the upper spiracular margin. The eyes are usually protruded above the head in juveniles and young, and may remain so, or becoming partly embedded and less protruded in adults. Eyeball remaining embedded throughout life is considered as phylogenetically informative character, and included in the present study.

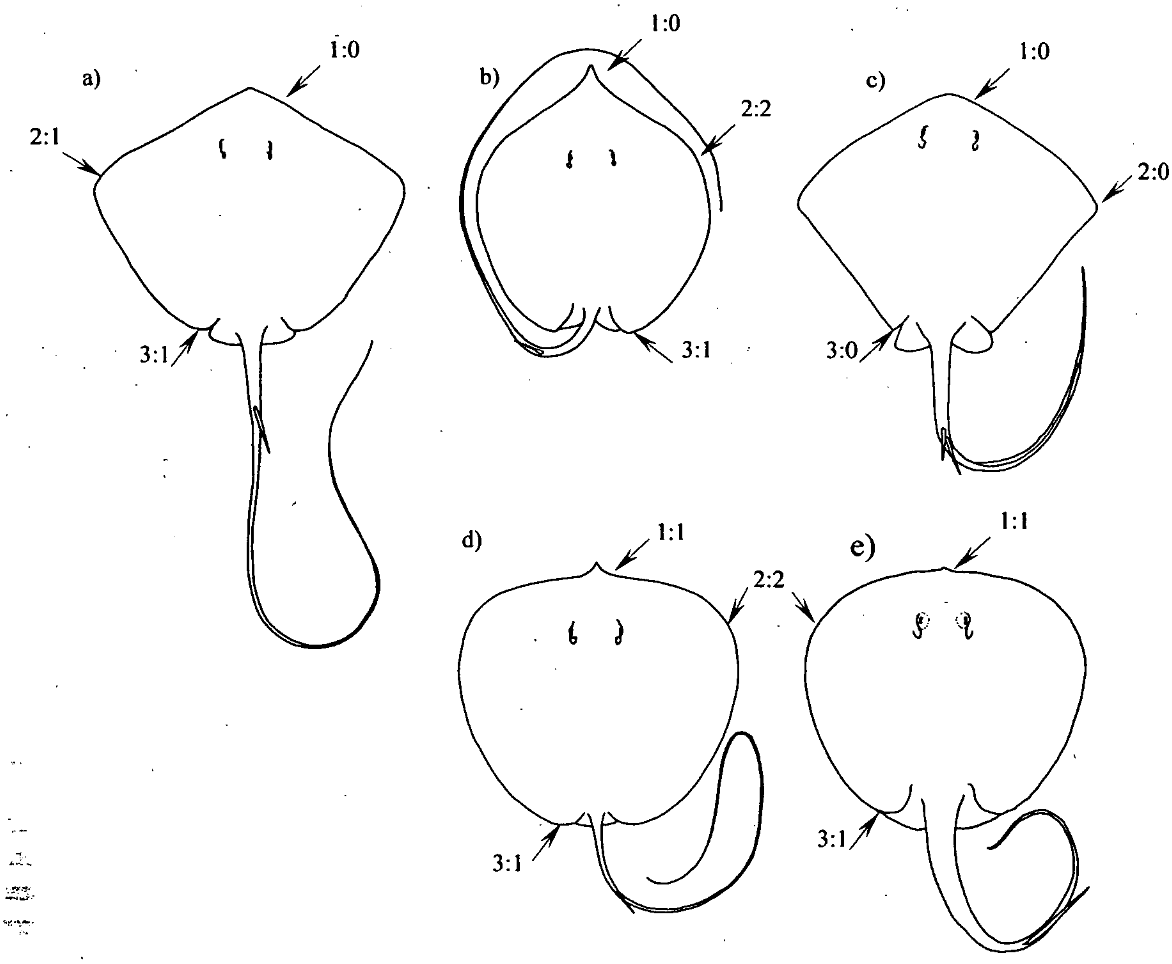


Figure 3.2.1. Disc shapes. a) *Himantura fai*, b) *H. oxyrhyncha*, c) *Dasyatis kuhlii*, d) *H. chaophraya*, e) *H. schmardae*. Numbers represent character and character state. a,c,d: redrawn from Last & Stevens (1994); e: redrawn from Bigelow & Schroeder (1953).

The spiracles may be positioned laterally or dorsolateraly on the head, and their size may be smaller, equal to or larger than the eyeballs. A cartilaginous prespiracular flap controlling the opening and closing of the spiracle aperture is present in all the taxa examined. The size and shape of both the spiracles and prespiracular cartilage is a continuous character and are not included in the analysis.

4. *Orbits*. — Protruded or clearly demarcated from head, coded as state 0 (Figure 3.2.2a,b) (all Indo-Pacific *Himantura, D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, P. sephen, P.* sp., *H. pacifica, H. schmardae*); embedded in head, coded as state 1 (Figure 3.2.2c,d) (*D. zugei, D. violacea*).

5. *Spiracle*. — Dorsolateral position on head, coded as state 0 (*H. imbricata, H. signifer, H. walga, D. zugei*); lateral or vertically positioned on head, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-G, *D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

a) b) c) d)

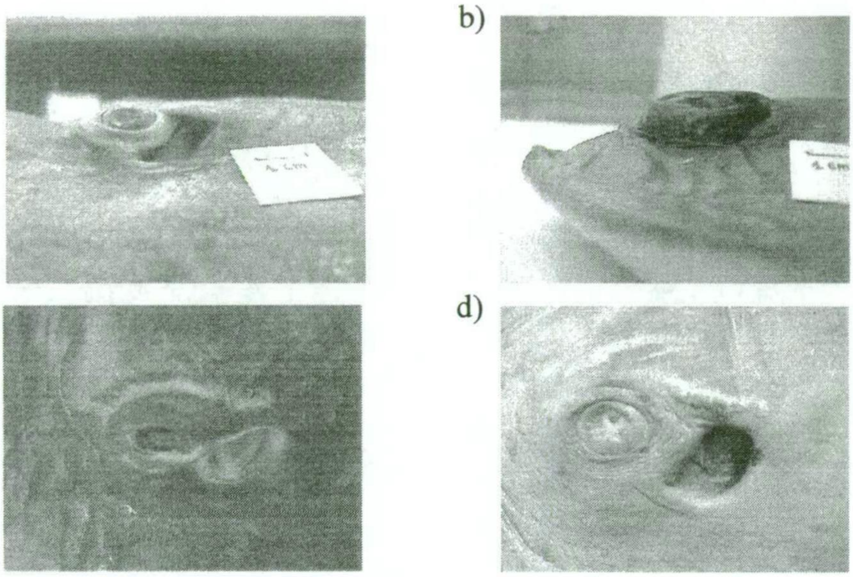


Figure 3.2.2. Orbit-spiracles. a) *Himantura gerrardi* CSIRO H4123.01, b) *Dasyatis kuhlii* CSIRO H5590.01, c) *D. zugei* CSIRO H4924.01, d) *D. violacea* CSIRO T450.

Oronasal (Figure 3.2.3)

The oronasal region consists of the mouth and nasal apertures including structures within these parts. A skirt-shaped nasal curtain which is formed of the expanded anterior nasal lobes covering the internasal space is present in all the taxa examined, except in the distant outgroup *R. typus*. The free posterior margin of nasal curtain is either not fringed or weakly to strongly fringed. The inner surface of the curtain is smooth, except for a small fleshy lobe on each posterolateral corner.

The nostrils have a single aperture, and a well-developed inner posterior lobe. The outer margin of the nostrils is smooth and void of any folds. Within each nostril are the nasal rachi, which is a series of plate-like structures held together by a thin longitudinal medial plate. The nasal rachi function to filter out particles in the water passing through the nostrils.

The jaws are anteriorly arched and undulating, and in normal closed position both upper and lower jaws interlock, with the upper jaw partly overlain by the lower jaw. The symphyseal tooth bands of the upper and lower jaws are usually slightly exposed even when the mouth is closed.

Inside the mouth, on the floor there are usually several fleshy projections, termed oral papillae. Within the Indo-Pacific *Himantura*, the oral papillae are entirely absent in two species (*H.* sp. E and *H.* sp. F). The oral papillae of one male specimen of *H. granulata* (688 mm disc width) from Pohnpei examined by Ishihara *et al.* (1993) was also recorded as absent, although present in five others. In the present study, all *H. granulata* specimens examined indicated the presence of oral papillae. The numbers of oral papillae may indicate intraspecific variation (e.g. Annandale 1909; Nishida & Nakaya 1990; this study), and therefore their importance limited in taxonomic value. Nevertheless, the phylogenetic significance of the oral papillae is recognized in its absence or presence (coded as polymorphic for *H. granulata* following Ishihara *et al.* (1993)). On the palate, there are always three longitudinal ridges and a pair of shorter lobes anterior to the outermost medial ridges. Although the palate ridges are relatively low when compared with the floor papillae, the central longest ridge appearing straight along the anterior-posterior axis of the oral cavity, and the two outer ridges and lobes arranged in a slight angle directed towards the central axis are usually readily observable.

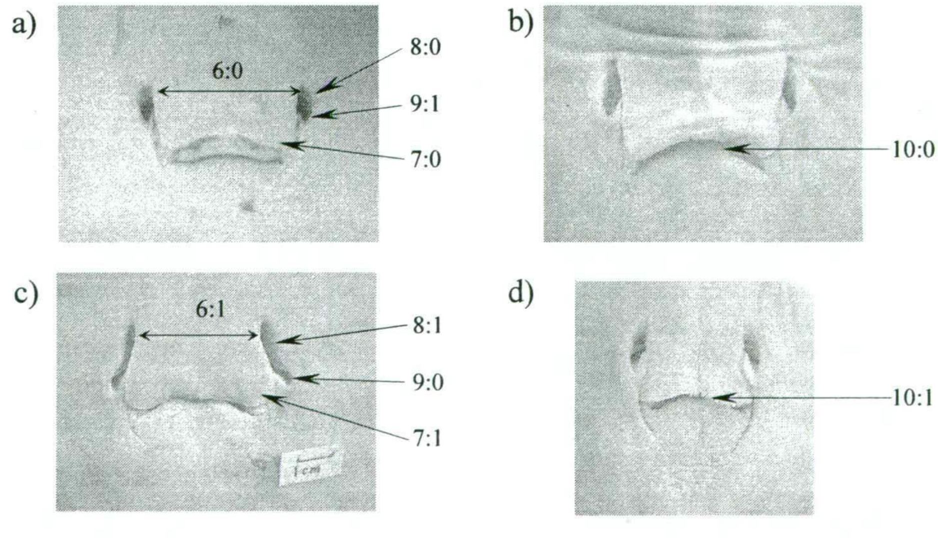


Figure 3.2.3. Oronasals. a) *Dasyatis acutirostra* HUMZ 107588, b) *D. zugei* CSIRO H4924.01, c) *Himantura uarnak* NTM S11507.006, d) *D. kuhlii* CSIRO H5590.01. Numbers represent character and character state.

6. *Anterior internasal distance vs. free posterior margin of nasal curtain.* — Wider, coded as state 0 (Figure 3.2.3a,b) (*D. acutirostra, D. zugei*); narrower, coded as state 1 (Figure 3.2.3c,d) (all Indo-Pacific *Himantura, D. kuhlii, D. laosensis, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

7. *Free posterior margin of nasal curtain.* — Not reaching to lower jaw, coded as state 0 (Figure 3.2.3a) (*D. acutirostra, D. violacea*); reaching lower jaw, coded as state 1 (Figure 3.2.3b,c,d) (all Indo-Pacific *Himantura, D. kuhlii, D. laosensis, D. leylandii, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

8. *Nostril.* — The nostrils are either circular, coded as state 0 (Figure 3.2.3a,b) (*D. acutirostra, D. violacea, D. zugei*); or slit-like, coded as state 1 (Figure 3.2.3c,d) (all Indo-Pacific *Himantura, D. kuhlii, D. laosensis, D. leylandii, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

9. *Nostril.* — Flared posterior end, coded as state 0 (Figure 3.2.3c) (all Indo-Pacific *Himantura, D. laosensis, P. sephen, P.* sp.); posterior end not flared, coded as state 1 (Figure 3.2.3a,b,d) (*D. acutirostra, D. kuhlii, D. leylandii, D. violacea, D. zugei, H. pacifica, H. schmardae*).

10. *Medial indentation of lower jaw.* — Absent or only with weak concavity, coded as state 0 (Figure 3.2.3a,b) (*H.* sp. G, *D. acutirostra, D. zugei, P. sephen, P.* sp.); present, coded as state 1 (Figure 3.2.3c) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides,H. signifier, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-F, *D. kuhlii, D. laosensis, D. leylandii, D. violacea, H. pacifica, H. schmardae*); both states were observed in *H. imbricata*, so this character was coded as polymorphic for this taxon.

11. *Oral papillae.* — Absent, coded as state 0 (*H.* sp. E-F, *D. acutirostra, D. zugei*); present, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-D, *H.* sp. G, *D. kuhlii, D. laosensis, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*). Both states were observed in *H. granulata* (Ishihara *et al.* 1993).

Pelvic-fin (Figure 3.2.4) *and clasper* (Figures 2.1.8, 3.2.5)

The pelvic-fins are paired and single lobed, and are almost entirely overlapped by the pectoral-fins. In males, the margin along the pelvic-fin insertion is modified to form the male copulatory organ, the claspers.

Claspers of the male elasmobranchs were not found in the Paleozoic elasmobranchs, their first appearance being in the Triassic hybodonts, so that internal fertilization must be considered a late development (White 1937). Thus, White signalled the phylogenetic significance of the structure of the claspers, which she specifically referred to the basal structures of the clasper skeleton (mixopterygia) and the general plan of the axial cartilages. Hulley (1972) later noted that it is the distal end of the clasper which is important in the systematics of lower taxa. According to him, although there were numerous anatomical studies on the claspers of rajids by various investigators, detailed comparative anatomical studies (of claspers) were lacking prior to his 1972 publication. In the few selected studies of myliobatoid clasper structure (Compagno & Roberts 1982; Capape 1983; Taniuchi & Ishihara 1990; Nishida 1990), the clasper glans is consistently relatively simple, generally consisting of only the dorsal and ventral lobes, and the hypopyle lacking any structures inside it.

As observed in this study, claspers of juvenile Indo-Pacific *Himantura* species are similar in overall shape, the clasper structures and shapes gradually developing during growth until it reach maturity. At maturity, the clasper is a relatively hardened, rod-like structure with its posterior tip extending beyond the posterior margin of the pelvic-fins. On the dorsal surface of each clasper are two grooves, the clasper groove (Compagno & Roberts 1982; Taniuchi & Ishihara 1990), and the pseudosiphon (Hulley 1972; Compagno & Roberts 1982). The clasper groove is a longitudinal dorsomedial groove with two terminal openings, the hypopyle (Leigh-Sharpe 1920), and below it, the pseudopera (Taniuchi & Ishihara 1990). The apopyle (Leigh-Sharpe 1920; Stehmann 1970; Compagno & Roberts 1982; Taniuchi & Ishihara 1990) is the anterior proximal opening of the clasper, in the region of the opening of the secretion passage of the clasper gland; it is connected to the hypopyle by an open posteriorly curved clasper groove. The pseudosiphon, termed 'SAC2' by Nishida (1990), is the shorter dorsolateral groove, which is really just a cavity with an oval aperture, and unconnected to the clasper groove (Figure 2.1.8). The ventral surface of the clasper is entirely smooth.

Within the Indo-Pacific *Himantura* taxa, the inside of the hypopyle is smooth, without any structure(s) inside it. A structure termed rhipidion is present inside the hypopyle of the skate clasper (e.g. McEachran & Last 1994). On the other hand, a pseudorhipidion (Capape 1983; McEachran & Last 1994), termed 'small flap' by Nishida (1990), which is a fleshy extension of the proximal end base of the hypopyle (Figure 3.2.5u-x), was described from certain dasyatid claspers, i.e.

Dasyatis centroura, D. kuhlii, D. pastinaca and *D. violacea* (Capape 1983; Nishida 1990). However, the presence or absence of this structure, or other differences observed in the clasper morphology was not used by Nishida (1990) in his phylogenetic analysis of the myliobatoids, due to a lack of study materials.

In this study, the pseudorhipidion was observed in several of the Indo-Pacific *Himantura*, i.e. *H. granulata* (Figure 3.2.5d), *H. uarnacoides* (Figure 3.2.5o), and *H.* sp. A (Figure 3.2.5s), and in *D. kuhlii* (Figure 3.2.5u), *D. leylandii* (Figure 3.2.5v), and in two other dasyatid species not included in the phylogenetic analyses of the present study, i.e. *D. fluviorum* (Figure 3.2.5w) and *D. longus* (Figure 3.2.5x). However, the structure observed in the Indo-Pacific *Himantura* appears distinct from that observed in the *Dasyatis* because in the latter, it is more lobe-like and demarcated by a deep notch on the margin of the anterior end of the hypopyle. Correspondingly, the pseudorhipidion is considered as absent in these Indo-Pacific *Himantura*.

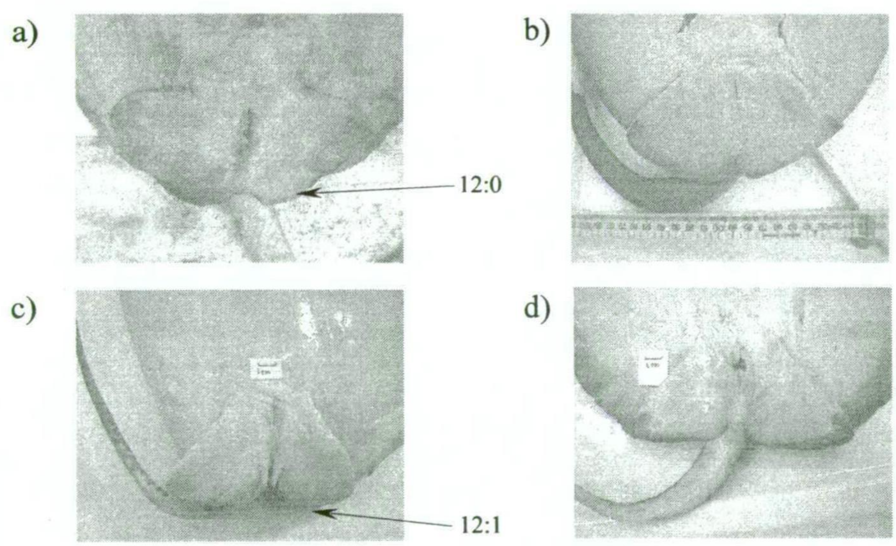


Figure 3.2.4. Pelvic-fins. a) *Dasyatis laosensis* MTUF uncatalogued frozen specimen, b) *Himantura pacifica* ROM ICH66838, c) *H. uarnak* NTM S11507.006, d) *H. pastinacoides* CSIRO H5479.12. Numbers represent character and character state.

12. *Pelvic-fins*. — Free rear tip posterior to apex, coded as state 0 (Figure 3.2.4a,b) (*D. laosensis, D. violacea, H. pacifica, H. schmardae*); free rear tip level or anterior to apex, coded as state 1 (Figure 3.2.4c,d) (all Indo-Pacific *Himantura, D. acutirostra, D. kuhlii, D. leylandii, D. zugei, P. sephen, P.* sp.).

13. *Clasper of mature males.* — Tip rounded or bluntly pointed appearing rod-like, coded as state 0 (Figure 3.2.5a-t) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A, *H.* sp. E., *H.* sp. G, *D. violacea, D. zugei*); tip pointed, coded as state 1 (Figure 3.2.5u,v) (*D. kuhlii, D. leylandii*). Unknown state for *H. oxyrhyncha, H.* sp. B-D, *H.* sp. F, *D. acutirostra, D. laosensis, P. sephen, P.* sp., *H. pacifica,* and *H. schmardae.*

14. *Clasper, pseudosiphon.* — Pseudosiphon absent, coded as state 0 (*D. acutirostra, D. laosensis, D. violacea, D. zugei*); pseudosiphon present and positioned on anterior of hypopyle near clasper groove, coded as state 1 (Figure 3.2.5u-v) (*D. kuhlii, D. leylandii*); pseudosiphon present and positioned on inner margin of clasper, coded as state 2 (Figure 3.2.5a-t) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-E, *H.* sp. G). Unknown state for *H. oxyrhyncha, H.* sp. F, *P. sephen, P.* sp., *H. pacifica,* and *H. schmardae.*

15. *Clasper, pseudorhipidion.* — Present coded as state 0 (Figure 3.2.5u-x) (*D. kuhlii, D. leylandii, D. violacea*); absent coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-E, *H.* sp. G). Unknown state for *H. oxyrhyncha, H.* sp. F, *D. acutirostra, D. laosensis, D. zugei, P. sephen, P.* sp., *H. pacifica,* and *H. schmardae.*

Tail

The tail is whip-like, variably shaped in cross section among species, but generally tapers to a fine point. Although the skin fold is lacking within the Indo-Pacific *Himantura*'s, a weak keel may be present, which is usually readily observed in preserved specimens. The weak longitudinal keel along a groove may be present on the ventral surface of the tail, beginning from the sting base and ending near the tail tip, or keels may be present on each side of the dorsolateral surface of the tail.

The homology between the tail skin fold and the cartilaginous caudal fins was established by Nishida (1990). Thus, following Nishida (1990: character 80) and Rosenberger (2001a: characters 4 & 5), dorsal and ventral tail skin fold characters are included in the character matrix. However, the state of these characters is modified to treat the presence of a rudimentary non-cartilaginous skin fold, i.e. 1 mm or less in height, as in *D. acutirostra*, as absent.

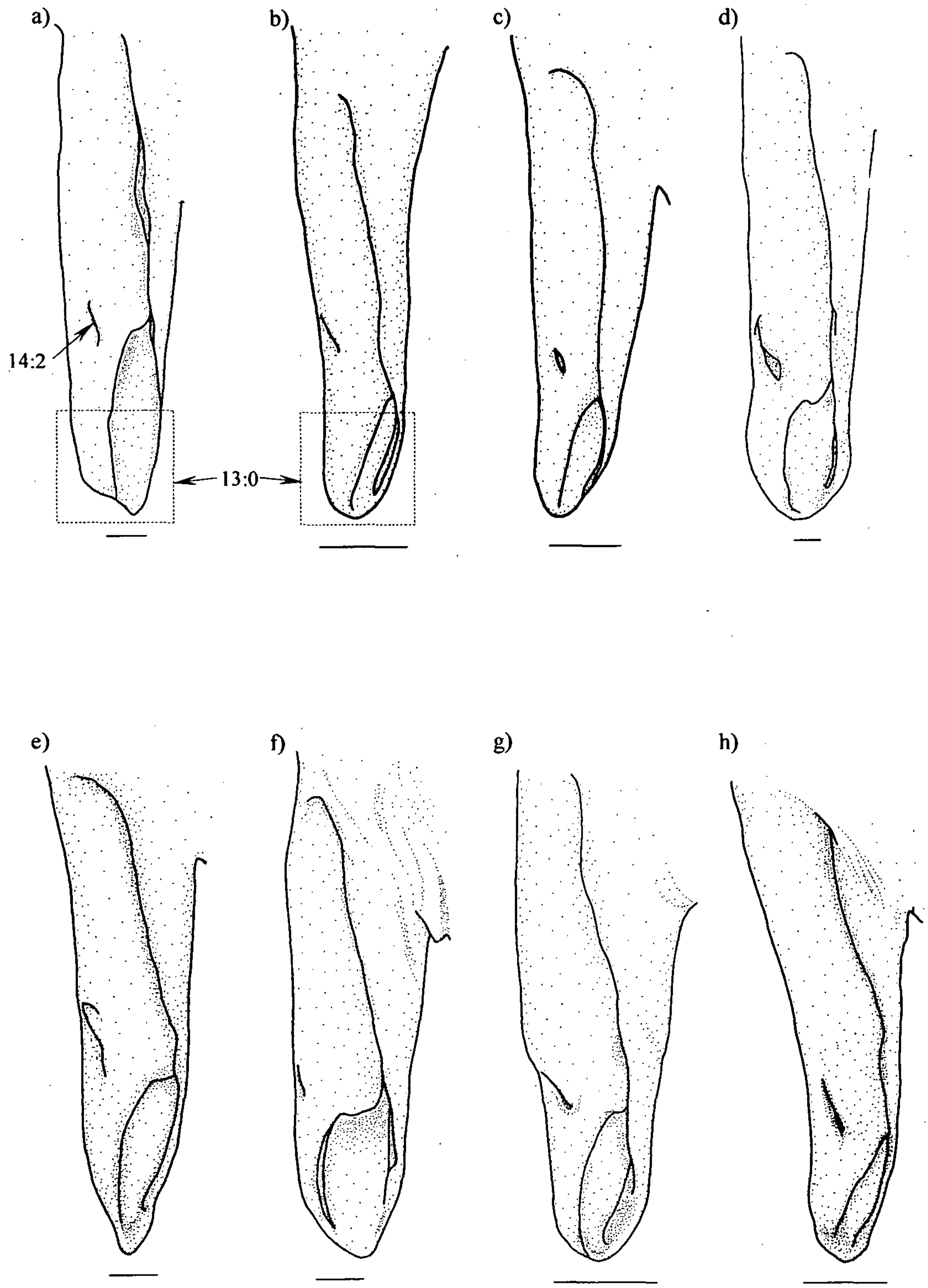


Figure 3.2.5. Right claspers (dorsal view). a) *H. fai* CSIRO H4426.33, b) *H. gerrardi* CSIRO H5284.03, c) *H. gerrardi* CSIRO H4918.02, d) *H. granulata* CSIRO H4426.32, e) *H. jenkinsii* CSIRO H2906.01, f) *H. jenkinsii* CSIRO H5585.01, g) *H. pastinacoides* UMS MMSK40, h) *H. toshi* CSIRO H1222.1. Bars 10 mm. Numbers represent character and character states.

continued...

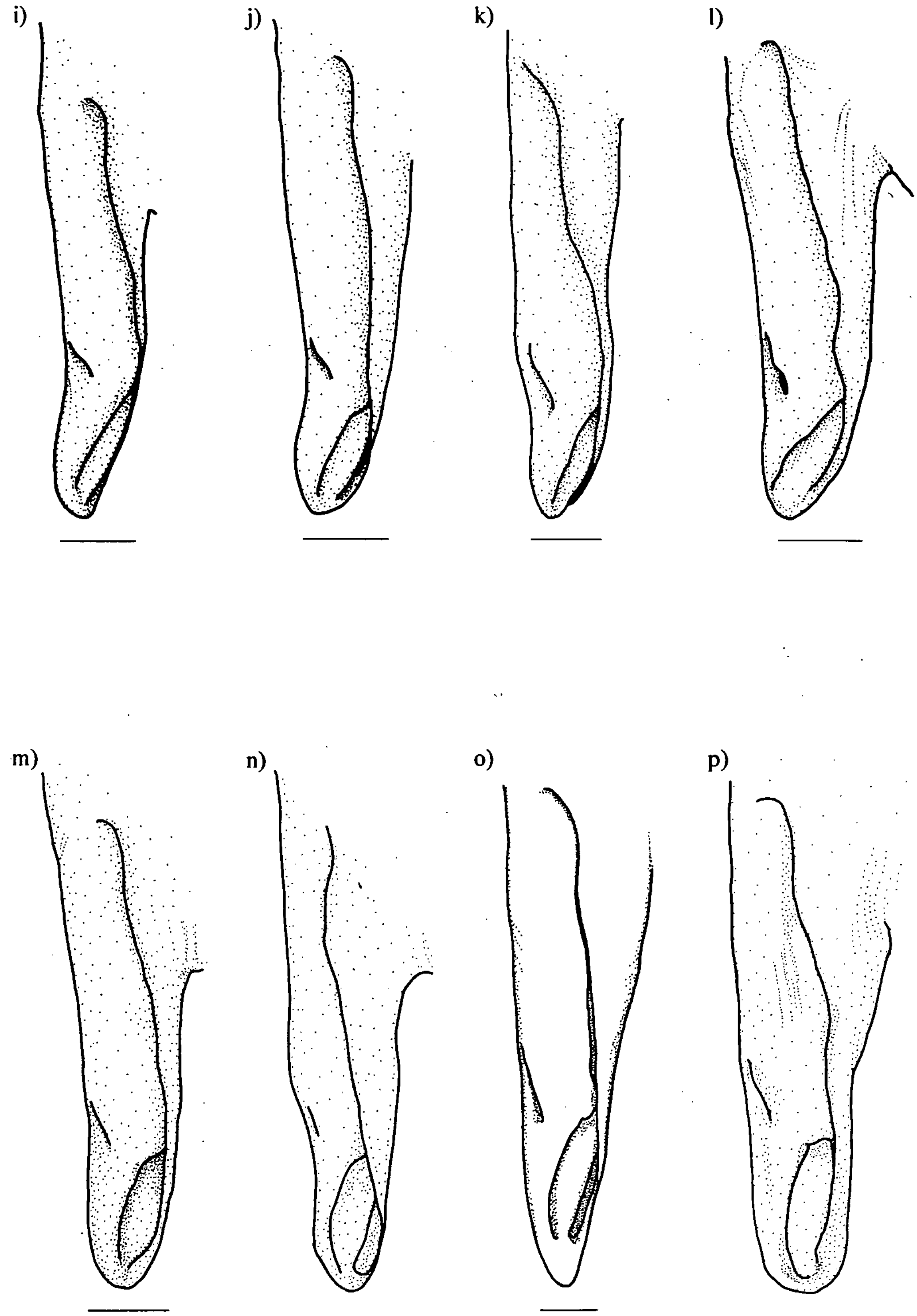


Figure 3.2.5. Continued. i) *H. toshi* CSIRO H5586.02, j) *H. toshi* CSIRO H5586.03, k) *H. toshi* CSIRO H5586.04, l) *H. toshi* CSIRO H5587.01, m) *H. toshi* CSIRO H5588.01, n) *H. toshi* CSIRO H5589.01, o) *H. uarnacoides* CSIRO H4426.31, p) *H. uarnak* CSIRO H5476.03. Bars 10 mm.

continued...

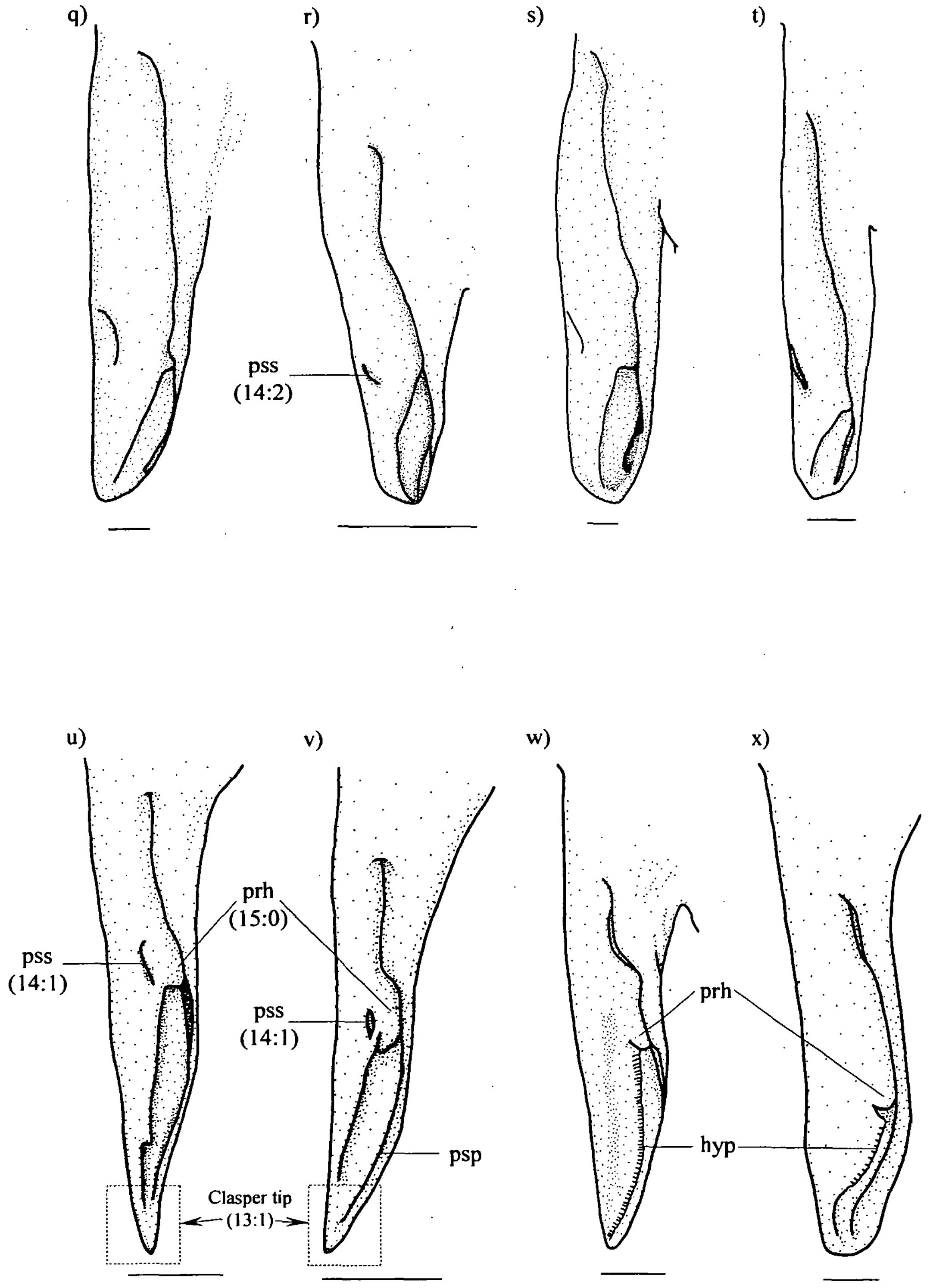


Figure 3.2.5. Continued. q) *H. undulata* CSIRO H5481.01, r) *H. walga* CSIRO H5474.02, s) *H.* sp. A CSIRO H3903.02, t) *H.* sp. E CSIRO H5155.01, u) *D. kuhlii* CSIRO H5590.01, v) *D. leylandii* CSIRO H5590.02, w) *D. fluviorum* CSIRO H5286.01, x) *D. longus* LACM 49779-3. Bars 10 mm. hyp: hypopyle, prh: pseudorhipidion, psp: pseudopera, pss: pseudosiphon. Numbers in parentheses represent character and character states.

16. *Cross section of tail base.* — Depressed, coded as state 0 (*H. granulata, H. imbricata, H. pastinacoides, H. signifer, H. uarnacoides, H. walga, H.* sp. E-G, *D. kuhlii, D. laosensis, D. leylandii, P. sephen, P.* sp., *H. pacifica, H. schmardae*); circular, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. jenkinsii, H. oxyrhyncha, H. toshi, H. uarnak, H. undulata, H.* sp. A-D, *D. acutirostra, D. violacea, D. zugei*).

17. *Cross section of tail at sting base.* — Constricted, coded as state 0 (*H. granulata, H. imbricata, H. signifer, H. walga, H.* sp. G, *D. violacea, D. zugei, P. sephen, P.* sp.); not constricted, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-F, *D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, H. pacifica, H. schmardae*).

18. *Tail dorsal fold.* — Present, coded as state 0 (*D. kuhlii, D. laosensis, D. leylandii*); absent or rudimentary, coded as state 1 (all Indo-Pacific *Himantura, D. acutirostra, D. violacea, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

19. *Tail ventral fold.* — Present, coded as state 0 (*D. kuhlii, D. laosensis, D. leylandii, D. violacea, D. zugei, P. sephen, P.* sp.); absent or rudimentary, coded as state 1 (all Indo-Pacific *Himantura, D. acutirostra, H. pacifica, H. schmardae*).

Squamation

The study of the developmental stages of squamation in Chapter 2, revealed specific patterns of denticle arrangement among groups (sub-complexes) within the ingroup. A typical pattern observed in stingray squamation is that several denticle types are consistently confined to the mid-disc, or along the trunk. Most types however, are evenly distributed on the entire dorsal surface, or on the tail.

The primary denticle band usually becomes inconspicuous after an individual stingray reaches a certain size, depending on species. Therefore, presence or absence of the primary denticle band (described in Chapter 2) was not considered as phylogenetically informative due to the difficulty in coding for this character. On the other hand, the secondary and tertiary denticle bands are conspicuous throughout life. The mid-scapular denticles, are usually either present or absent in both young and adult stages, although both states are found in several species.

The presence of enlarged denticles or thorns along the midline of the tail (Rosenberger 2001a: character 6) is noted in several species. These consist of independent row(s) of thorns which develop early in the life stage, and are different in shape and/or size to the embryological, primary and secondary denticles.

Therefore, presence or absence of this character is considered as phylogenetically informative. Similar enlarged denticles may be observed only in large (>1 m disc width) mature specimens of several species, i.e. *H. fai, H. granulata, H. uarnak* and *H.* sp. A. However, such denticles are considered as not homologous to those which develop earlier in life. Accordingly, enlarged denticles along the midline of the tail is coded as absent in these species.

20. *Secondary denticle band in sub-adults and adults.* — Absent, coded as state 0 (*D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. violacea, D. zugei*); Present, coded as state 1 (all Indo-Pacific *Himantura, P. sephen, P.* sp., *H. pacifica, H. schmardae*).

21. *Tertiary denticle band.* — Absent, coded as state 0 (*H. imbricata, H. jenkinsii, H. pastinacoides, H. toshi, H. uarnacoides, H. walga, H.* sp. E-F, *D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. violacea, D. zugei, P. sephen, P.* sp.); present, coded as state 1 (*H. chaophraya, H. fai, H. granulata, H. oxyrhyncha, H. signifer, H. uarnak, H. undulata, H.* sp. A, *H.* sp. G, *H. schmardae*). Unknown state for *H. gerrardi, H.* sp. B-D and *H. pacifica.*

22. *Enlarged mid-scapular denticles in young and adults.* — Absent, coded as state 0 (*H. fai, D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. violacea, D. zugei*); present, coded as state 1 (*H. chaophraya, H. gerrardi, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-G, *P. sephen, P.* sp., *H. pacifica, H. schmardae*). Both states were observed in *H. granulata, H. imbricata* and *H. walga*, so this character was coded as polymorphic for these taxa.

23. *Enlarged row of denticles along trunk to midline of tail in sub-adults and adults* (modified from Rosenberger 2001a: character 6). — Absent, coded as state 0 (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H.* sp. A-F, *H. pacifica, H. schmardae*); present, coded as state 1 (*H. imbricata, H. jenkinsii, H. oxyrhyncha, H. signifer, H. walga, H.* sp. G, *D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. violacea, D. zugei*). Both states were observed in *H. undulata, P. sephen* and *P.* sp., so this character was coded as polymorphic for these taxa.

3.2.1.2 Internal morphology

Ventral lateral line canal patterns (Figure 3.2.6)

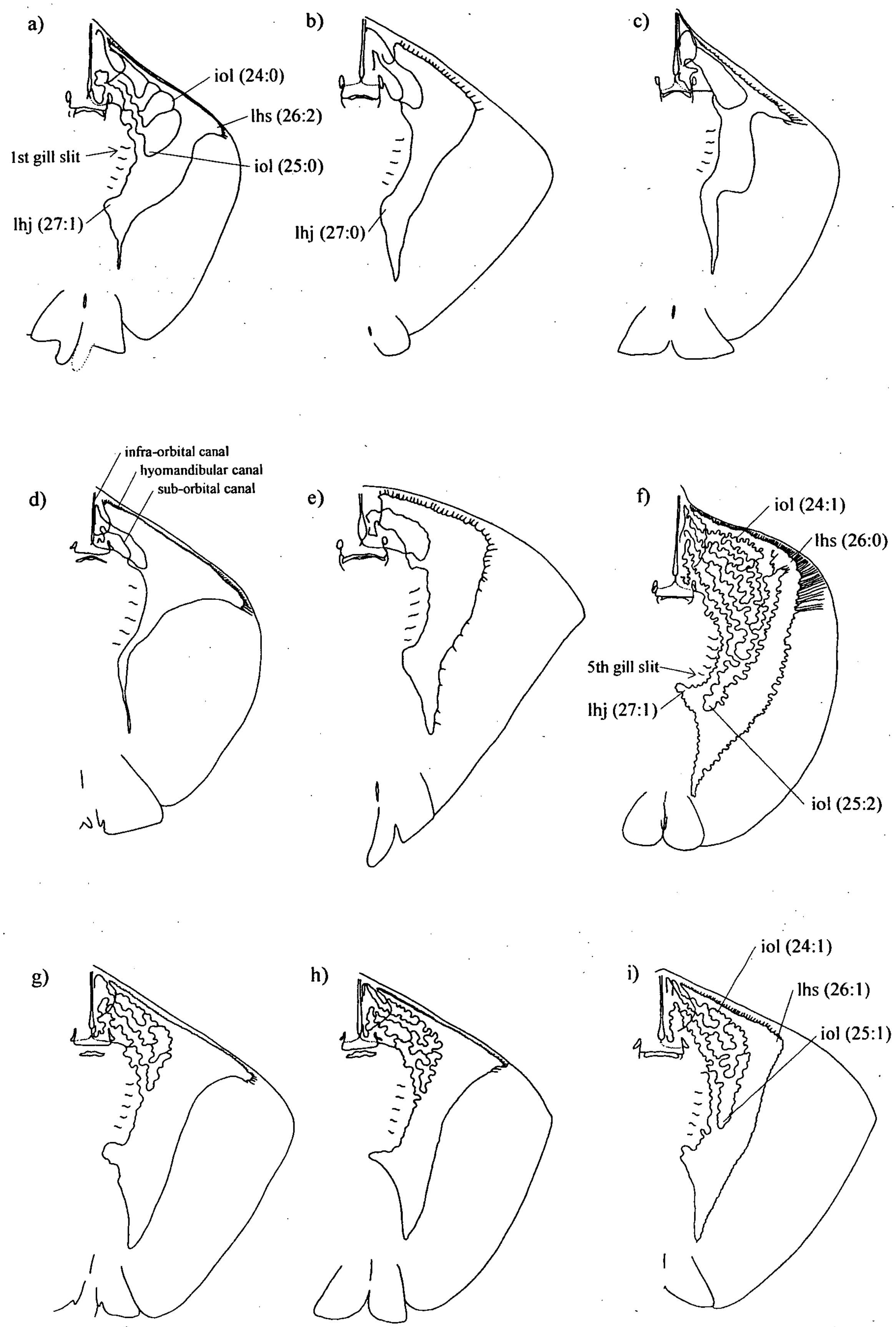
The lateral line is part of the acousticolateralis or hydrodynamic sensory system in fishes (see Bleckmann & Hofmann 1999; Kemp 1999). Garman (1888) discussed the system in elasmobranchs extensively, but apparently was uncertain about its homology between the galeas (sharks), selachians (rays) and holocephalans (chimaeras). Melouk (1959) attempted to demonstrate the homology of this system in the selachians based on ontogenetic studies using the blue-spotted stingray *D. kuhlii*, and correlated his findings with those in more primitive and specialized groups. His results also showed that the final distributional pattern of sensory canals was achieved in the advanced form of an embryo. However, he noted that secondary structural changes (i.e. branching, division and fusion) of the lateral line canals continued to develop in later stages. More recently, Northcutt (1989) studied the phylogeny of lateral lines and their innervation in fishes, including chondrichthyans, but suggested more studies are needed to homologize many of the lateral lines in batoids and holocephalans to those in sharks.

Systematic studies of elasmobranchs utilizing the variation in the pattern of the lateral line canals appear to be first exploited by Chu and Wen (1979). However, it was not until after Lovejoy (1996) that others (McEachran *et al.* 1996; Rosenberger 2001a) have begun to explore this character further. In particular are variations of the ventral lateral line canal patterns. Thus, following Lovejoy, and McEachran *et al.*, three primary ventral lateral line canals in stingrays, i.e. the hyomandibular canal, infra-orbital canal, sub-orbital canal, including the respective components are recognized (Figure 3.2.6). In addition to the characters of the ventral lateral line canals utilized in these earlier works, a new character, i.e. the lateral hook of the jugular component of the hyomandibular canal and its degree of angularity, whether shallow or deep, is introduced and included in the character matrix.

In their respective studies, Lovejoy (1996) and McEachran *et al.* (1996) also both included characters of the dorsal lateral line. The character used by Lovejoy (1996: character 1), i.e. extension of the dorsal tubules of the pleural loop towards the borders of the disc is an autopomorphic character seen in *Gymnura*. McEachran *et al.* (1996: character 19) used the character scapular loops present; this character appears invariable in stingrays (Garman 1888; Chu & Wen 1979; McEachran *et al.* 1996), and it was not extensively investigated in the present study.

24. *Infra-orbital loop* (modified from Lovejoy 1996: character 4; McEachran *et al.* 1996: character 15). — Simple, not reticulated, coded as state 0 (Figure 3.2.6a-e) (*H. walga, D. kuhlii, D. leylandii, D. violacea, D. zugei, P. sephen, H. pacifica, H. schmardae*); extensive reticulation and looping, coded as state 1 (Figure 3.2.6f-q) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-G, *D. acutirostra*). Unknown state for *H. imbricata, D. laosensis,* and *Pastinachus* sp.

Figure 3.2.6. Ventral lateral line canal patterns. a) *H. walga* CSIRO H5474.01, b) *D. leylandii* CSIRO H3361.07, c) *D. zugei* CSIRO H4924.20, d) *P. sephen* CSIRO H5480.03, e) *D. violacea* CSIRO T450, f) *H. chaophraya* CSIRO H5283.01, g) *H. gerrardi* CSIRO H4926.10, h) *H. gerrardi* CSIRO H5612.01, i) *H. jenkinsii* CSIRO H5475.01, j) *H. oxyrhyncha* ZRC 42984, k) *H. pastinacoides* CSIRO H5471.01, l) *H. signifer* ZRC 42547, m) *H. toshi* CSIRO T698, n) *H. uarnacoides* CSIRO H5616.01 and CSIRO H5616.02, o) *H. uarnak* CSIRO H5477.02, p) *H. undulata* CSIRO H5482.02, q) *H.* sp. E CSIRO H4916.01. iol: infra-orbital loop of the infra-orbital and sub-orbital canals, lhj: lateral hook of the jugular component of hyomandibular canal, lhs: lateral hook of the subpleural component of hyomandibular canal. Numbers in parentheses represent character and character state.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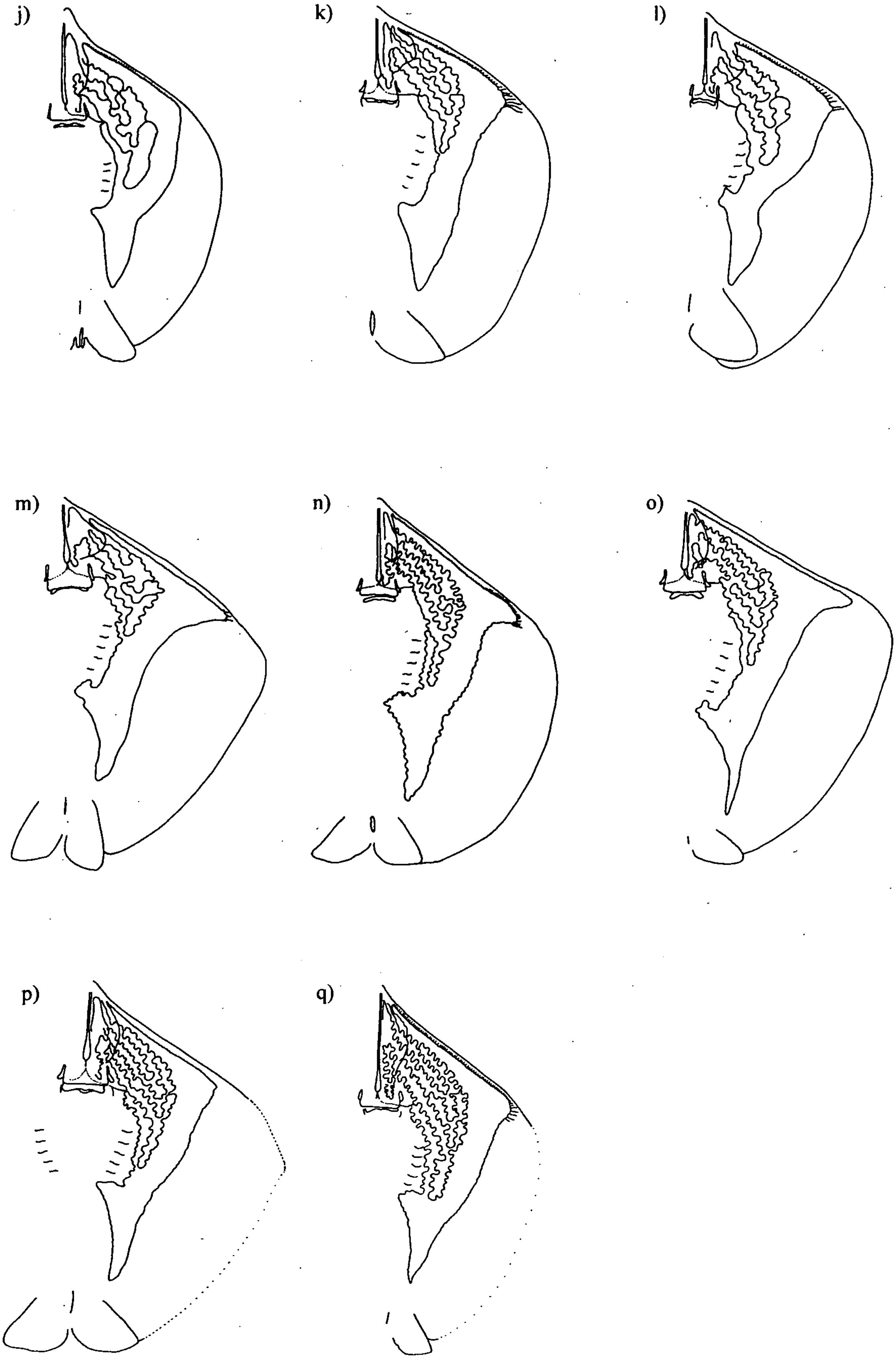
iol (24:0)
lhs (26:2)
1st gill slit
iol (25:0)
lhj (27:1)
b)
lhj (27:0)
c)
infra-orbital canal
hyomandibular canal
sub-orbital canal
d)
e)
f)
iol (24:1)
lhs (26:0)
5th gill slit
lhj (27:1)
iol (25:2)
g)
h)
i)
iol (24:1)
lhs (26:1)
iol (25:1)


j)
k)
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q)

25. *Infra-orbital loop* (modified from McEachran *et al.* 1996: character 15). — Anterior or slightly posterior to the first gill slit, coded as state 0 (Figure 3.2.6a-e,g-h,m) (*H. gerrardi, H. toshi, H. walga, D. kuhlii, D. leylandii, D. violacea, D. zugei, P. sephen, H. pacifica, H. schmardae*); extending to between first and fifth gill slit, coded as state 1 (Figure 3.2.6i-l,o-p) (*H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. uarnak, H. undulata, H.* sp. A, *H.* sp. F); extending beyond fifth gill slit coded as state 2 (Figure 3.2.6f,n,q) (*H. chaophraya, H. fai, H. uarnacoides, H.* sp. E). Unknown state for *H. imbricata, H.* sp. B-D, *H.* sp. G, *D. acutirostra, D. laosensis,* and *Pastinachus* sp.

26. *Lateral hook formed by subpleural component of hyomandibular canal* (modified from Lovejoy 1996: character 3; McEachran *et al.* 1996: character 16; Rosenberger 2001a: character 8). — Absent (broadly rounded), coded as state 0 (Figure 3.2.6e,f,j,l) (*H. chaophraya, H. granulata, H. oxyrhyncha, H. signifier, D. violacea, H. pacifica, H. schmardae*); shallow, coded as state 1 (Figure 3.2.6b,i,k,p,q) (*H. jenkinsii, H. pastinacoides, H. undulata, H.* sp. E-F, *D. kuhlii, D. leylandii*); deeply indented coded as state 2 (Figure 3.2.6a,c-d,g-h,m-o) (*H. fai, H. gerrardi, H. toshi, H. uarnacoides, H. uarnak, H. walga, H.* sp. A, *D. zugei, P. sephen*). Unknown state for *H. imbricata, H.* sp. B-D, *H.* sp. G, *D. acutirostra, D. laosensis*, and *Pastinachus* sp.

27. *Lateral hook formed by jugular component of hyomandibular canal.* — Shallow (broadly rounded), coded as state 0 (Figure 3.2.6b-d) (*D. leylandii, D. zugei, P. sephen, H. pacifica*); deep, coded as state 1 (Figure 3.2.6a,e-q) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifier, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A, *H.* sp. E-F, *D. kuhlii, D. violacea*). Unknown state for *H. imbricata, H.* sp. B-D, *H.* sp. G, *D. acutirostra, D. laosensis, Pastinachus* sp., and *H. schmardae.*

Neurocranium (Figures 2.1.5, 3.2.7, 3.2.8)

The following character analysis results are based on the division of the neurocranium into four external regions, i.e. the ethmoidal, orbital, otic and occipital regions (Gegenbaur *in* Compagno 1999d). Among the whip-tailed stingrays, the neurocranium is very similar in its outline shape, including the relative position of the various foramina (Miyake 1988; Yearsley 1988; Nishida 1990; Lovejoy 1996; this study, Figures 3.2.7, 3.2.8). Pre- and postorbital processes are present in all the taxa examined. A jugal arch on the lateral otic process of the otic region, reported as absent in the myliobatoids (Nishida 1990; McEachran *et al.* 1996) was observed in the single dissected specimen of *P. sephen* (CSIRO H5479.20). However, the character was excluded from the analysis because it is autapomorphic in this species.

Variations observed in the outline of the neurocranium and the shape of fontanelle were coded following Rosenberger (2001a: characters 11-16), and are included in the present character matrix. Other characters include those relating to variations of the processes in the ethmoidal and occipital regions, position of the anterior foramen for preorbital canal and state of the supraorbital crest.

28. *Anterior profile of neurocranium* (modified from Rosenberger 2001a: characters 11 & 12). — Strongly double convex, coded as state 0 (Figure 3.2.7a-c,z,aa) (*H. granulata, H. imbricata, H. signifer, H. walga, H.* sp. G, *D. kuhlii, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*); anterolaterally angular coded as state 1 (Figure 3.2.7d-y) (*H. chaophraya, H. fai, H. gerrardi, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-F, *D. zugei*). Unknown state for *D. acutirostra,* and *D. laosensis.*

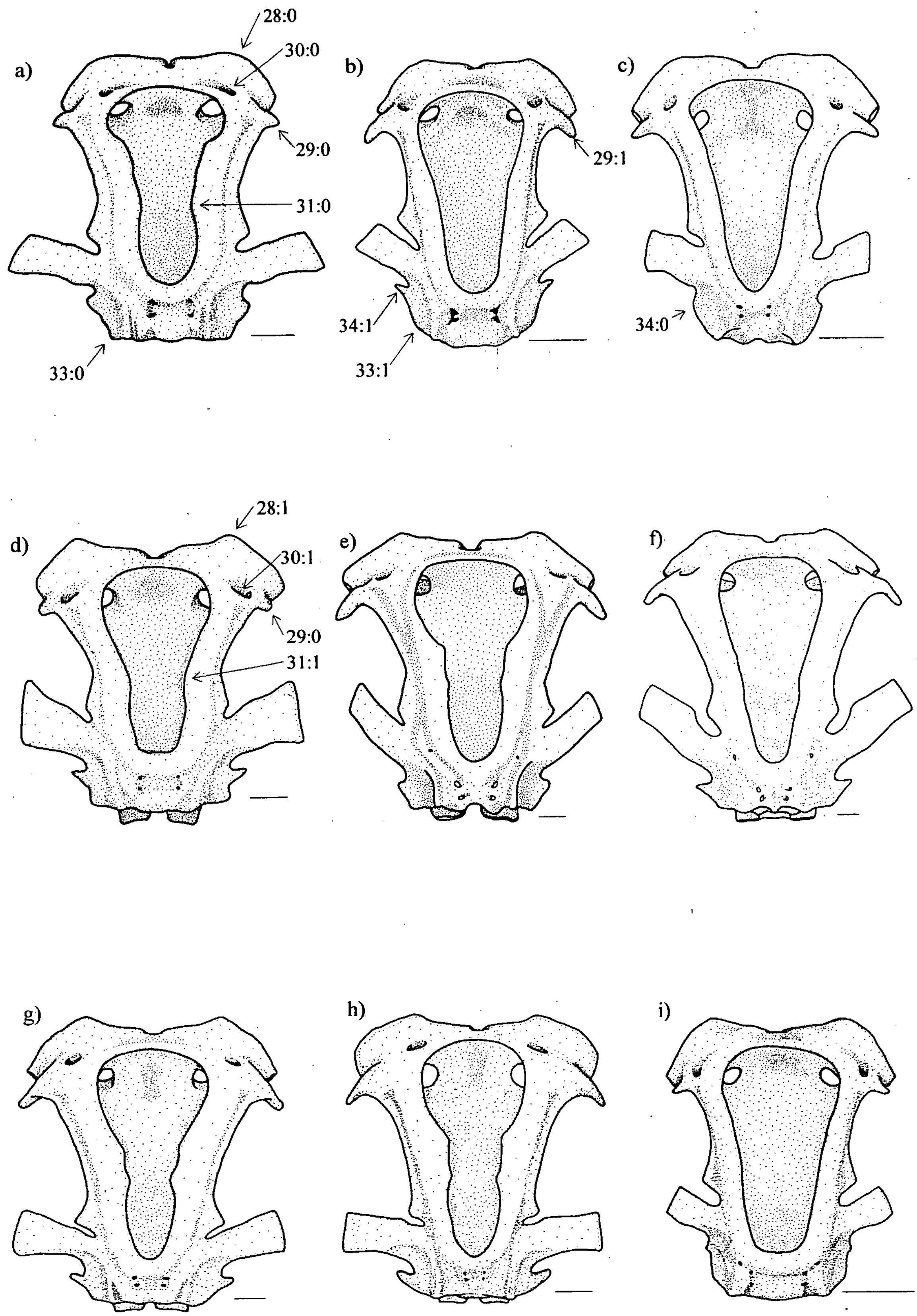
29. *Preorbital process.* — Short, knob-like, coded as state 0 (Figure 3.2.7a,d,x,y) (*H. chaophraya, H. granulata, H.* sp. E-F); moderately elongate, rod-like, coded as state 1 (Figure 3.2.7b,c,e-w,aa) (*H. fai, H. gerrardi, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-D, *H.* sp. G, *D. violacea, D. zugei, P. sephen, P.* sp.); extremely elongate, twig-like, coded as state 2 (Figure 3.2.7z) (*D. kuhlii, D. leylandii, H. pacifica, H. schmardae*). Unknown state for *D. acutirostra,* and *D. laosensis.*

30. *Position of anterior foramen for preorbital canal* (modified from Nishida 1990: character 85; McEachran *et al.* 1996: character 27). — Approximately level or forwards of anterior margin of dorsal fontanelle, coded as state 0 (Figure 3.2.7a,f-h,j-w) (*H. gerrardi, H. granulata, H. jenkinsii, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-D); markedly posterior of anterior margin of dorsal fontanelle, coded as state 1 (Figure 3.2.7b-e,i,z,aa) (*H. chaophraya, H. fai, H. imbricata, H. oxyrhyncha, H. signifer, H. walga, H.* sp. E-G, *D. kuhlii, D. leylandii, D. violacea, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*). Unknown state for *D. acutirostra,* and *D. laosensis.*

31. *Mid-region of dorsal fontanelle* (modified from Rosenberger 2001a: character 14). — Greatly constricted, coded as state 0 (Figure 3.2.7a,e,g-h,z) (*H. fai, H. granulata, H. jenkinsii, D. kuhlii, D. leylandii, D. violacea, H. pacifica, H. schmardae*); moderately constricted, coded as state 1 (Figure 3.2.7b-d,f,i-r,y,aa) (*H. chaophraya, H. gerrardi, H. imbricata, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-G, *D. zugei, P. sephen, P.* sp.). Unknown state for *D. acutirostra,* and *D. laosensis.*

32. *Supra-orbital crest* (modified from McEachran *et al.* 1996: character 26). — Reduced to a keel along the dorsolateral margin of the orbital region, coded as state 0 (*D. kuhlii, D. leylandii*); plate-like, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi*[a], *H. granulata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A, *H.* sp. E-G, *D. violacea, D. zugei, P. sephen, P.* sp.). Unknown state for *H. gerrardi*[b], *H. imbricata, H.* sp. B-D, *D. acutirostra, D. laosensis, H. pacifica,* and *H. schmardae.*

Figure 3.2.7. Neurocrania (dorsal view). a) *H. granulata* CSIRO CA1255, b) *H. signifer* ZRC 42547, c) *H. walga* CSIRO H5474.02, d) *H. chaophraya* CSIRO H5283.01, e) *H. fai* CSIRO H5484.01, f) *H. gerrardi* CSIRO H5284.04, g) *H. jenkinsii* CSIRO H3622.01, h) *H. jenkinsii* CSIRO H5475.01, i) *H. oxyrhyncha* ZRC 42984, j) *H. pastinacoides* CSIRO H5479.02, k) *H. toshi* CSIRO H1041.02, l) *H. toshi* CSIRO H5206.01, m) *H. toshi* CSIRO H5586.01, n) *H. toshi* CSIRO H5586.02, o) *H. toshi* CSIRO H5586.03, p) *H. toshi* CSIRO H5586.04, q) *H. toshi* CSIRO H5588.01, r) *H. toshi* CSIRO H5589.01, s) *H. uarnacoides* CSIRO H5470.01, t) *H. uarnak* CSIRO H5476.03, u) *H. undulata* CSIRO H5481.01, v) *H.* sp. A CSIRO H5478.01, w) *H.* sp. A CSIRO H5479.08, x) *H.* sp. E CSIRO H4916.01, y) *H.* sp. F CSIRO H5472.01, z) *D. kuhlii* CSIRO H5590.01, aa) *P. sephen* CSIRO H5479.20. Bars 10 mm. Numbers represent character and character state.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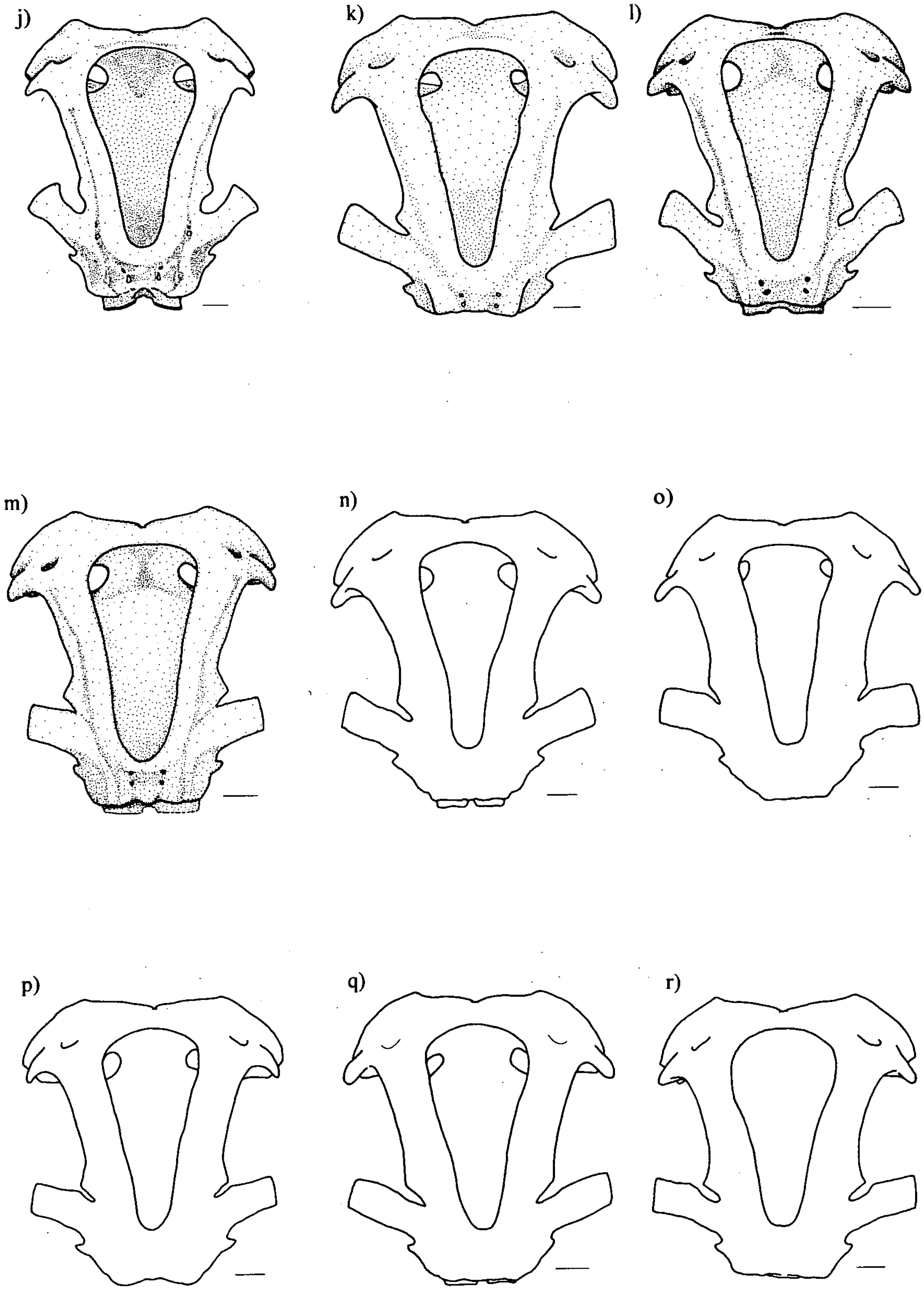
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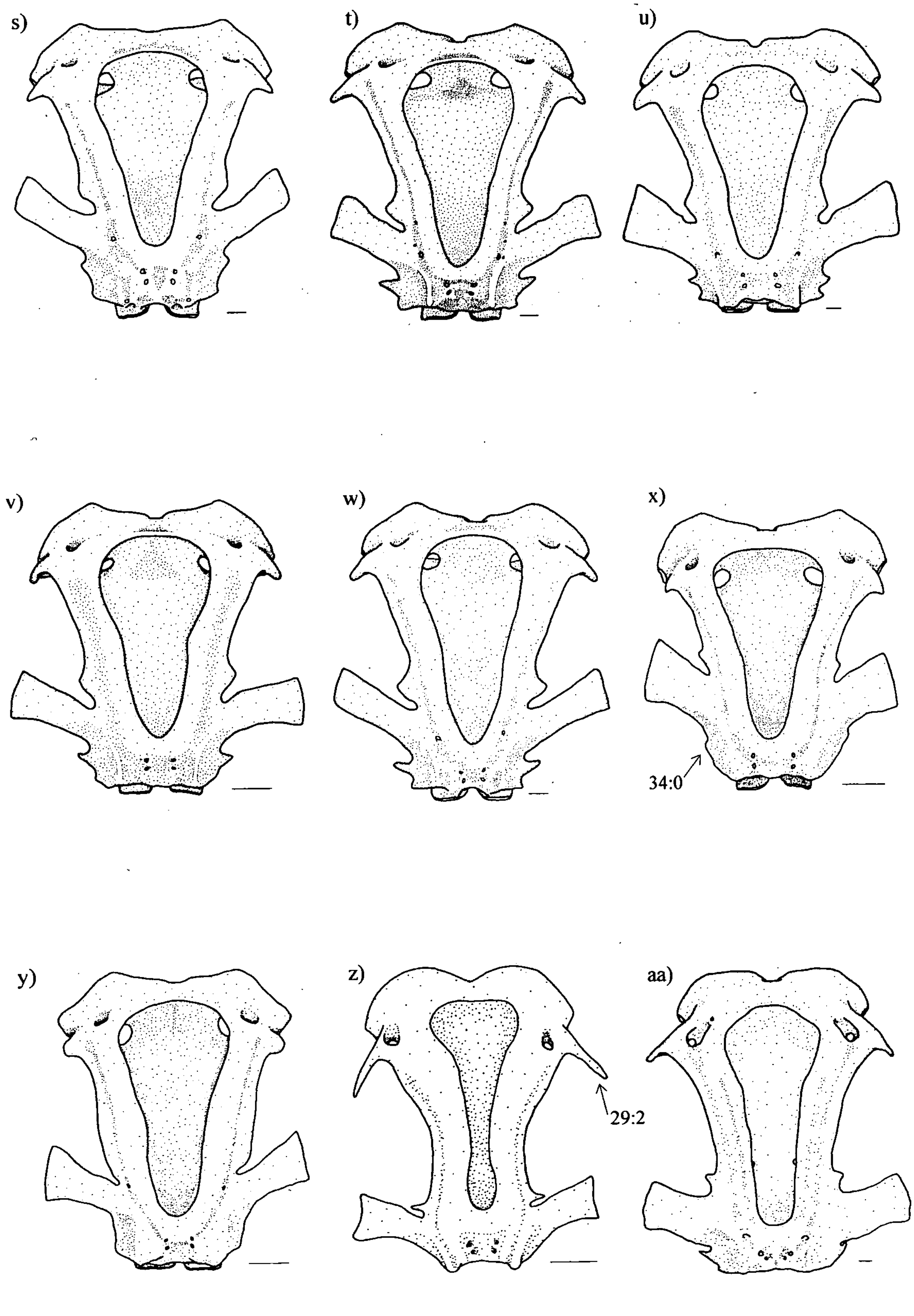
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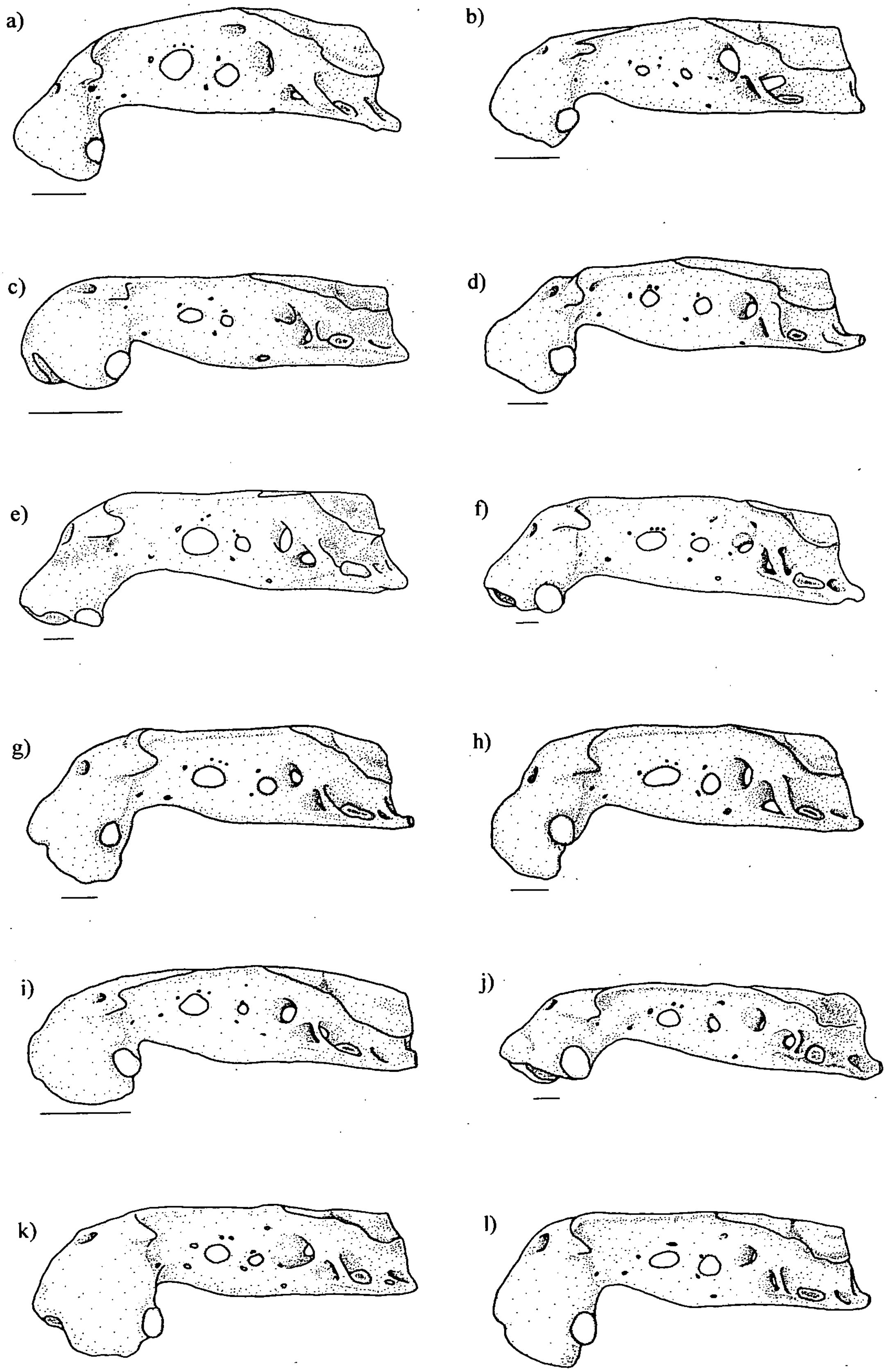
29:2
aa)

Figure 3.2.8. Neurocrania (lateral view). a) *H. granulata* CSIRO CA1255, b) *H. signifer* ZRC 42547, c) *H. walga* CSIRO H5474.02, d) *H. chaophraya* CSIRO H5283.01, e) *H. fai* CSIRO H5484.01, f) *H. gerrardi* CSIRO H5284.04, g) *H. jenkinsii* CSIRO H3622.01, h) *H. jenkinsii* CSIRO H5475.01, i) *H. oxyrhyncha* ZRC 42984, j) *H. pastinacoides* CSIRO H5479.02, k) *H. toshi* CSIRO H1041.02, l) *H. toshi* CSIRO H5206.01, m) *H. toshi* CSIRO H5586.01, n) *H. toshi* CSIRO H5586.03, o) *H. toshi* CSIRO H5586.04, p) *H. toshi* CSIRO H5588.01, q) *H. toshi* CSIRO H5589.01, r) *H. uarnacoides* CSIRO H5470.01, s) *H. uarnak* CSIRO H5476.03, t) *H. undulata* CSIRO H5481.01, u) *H.* sp. A CSIRO H5478.01, v) *H.* sp. A CSIRO H5479.08, w) *H.* sp. E CSIRO H4916.01, x) *H.* sp. F CSIRO H5472.01. Bars 10 mm.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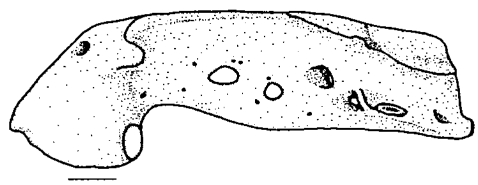

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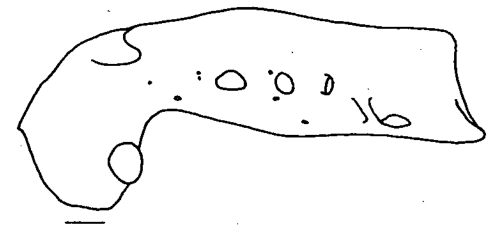

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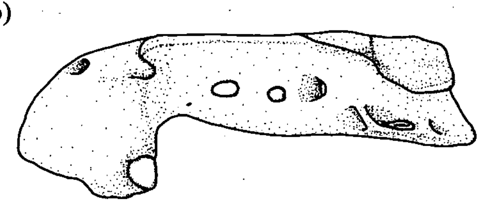

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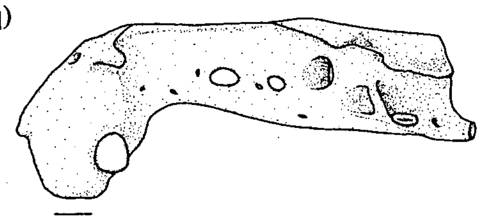

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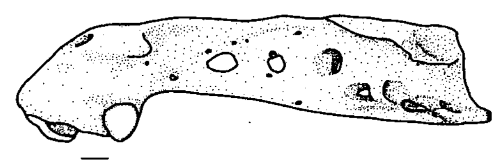

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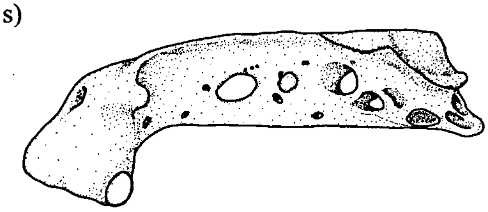

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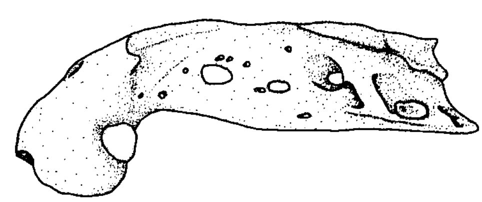

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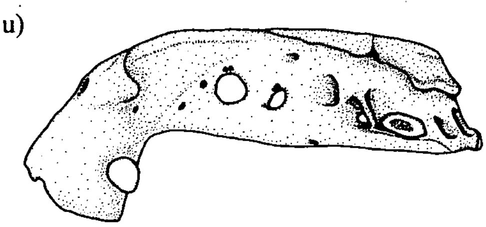

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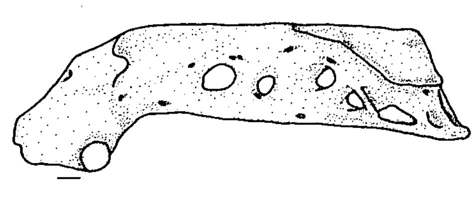

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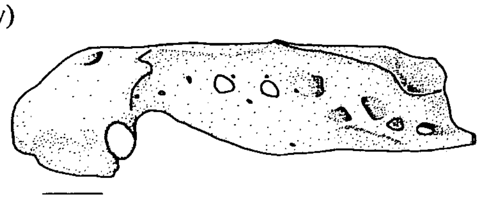
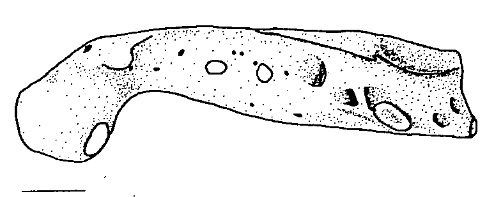


x)



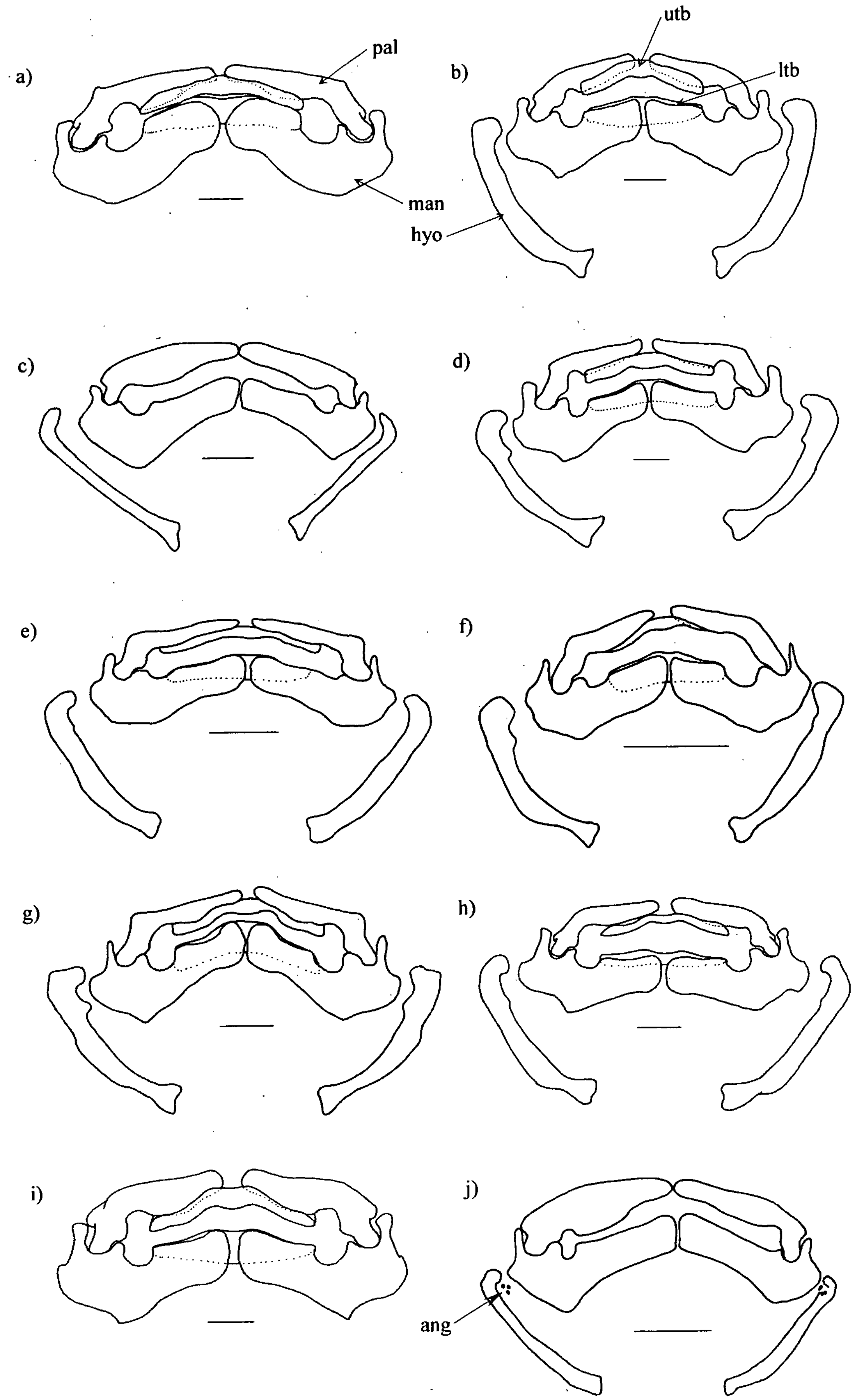
33. *Margin of sphenopterotic ridge in dorsal view.* — Angular, coded as state 0 (Figure 3.2.7a,d-w,y,z,aa) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-D, *H.* sp. F-G, *D. kuhlii, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*); broadly rounded, coded as state 1 (Figure 3.2.7b,c,x) (*H. signifer, H. walga, H.* sp. E, *D. zugei*). Unknown state for *D. acutirostra,* and *D. laosensis.*

34. *Process on sphenopterotic ridge.* — Absent, coded as state 0 (Figure 3.2.7c,x-z) (*H. walga, H.* sp. E-F, *D. kuhlii, D. leylandii, D. violacea, D. zugei, H. pacifica, H. schmardae*); present, coded as state 1 (Figure 3.2.7a-b,d-w,aa) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-D, *H.* sp. G, *P. sephen, P.* sp.). Unknown state for *D. acutirostra,* and *D. laosensis.*

Visceral arch

The visceral arch consists of the mandibular, hyoid, and branchial arches. The mandibular arch (Figure 3.2.9) of all the taxa examined in this study is comprised of a pair of palatoquadrate and mandibular (Meckelian) cartilages, with each pair closely articulated at the symphysis (Nishida 1990: character 97; McEachran *et al.* 1996: character 32), and forming the upper and lower jaws respectively. On each jaw, a tooth-band comprising small teeth arranged in diagonal rows is present (Nishida 1990: character 93; Lovejoy 1996: character 17; McEachran *et al.* 1996). The hyomandibular cartilages which form part of the hyoid arch, support the jaws in an anterolateral direction and is connected to it on the inner distal tip by ligaments. As in all other taxa, this cartilage is laterally compressed. However, among species, it is variable in length, thickness and degree of curvature or angularity between the origin and distal tips (Figure 3.2.9; McEachran *et al.* 1996: character 35). Other parts of the hyoid arch comprise smaller paired cartilages that are variably segmented (Nishida 1990: figure 27) and located posteroventral of the mandibular arch. The branchial arch comprises a single medial basibranchial plate and a series of 5 ceratobranchial cartilages attached laterally on each side (Nishida 1990: figure 27).

Figure 3.2.9. Mandibular arches (ventral view). a) *H. chaophraya* CSIRO H5283.01, b) *H. granulata* AMS I9763, c) *H. imbricata* NTM S13160.009, d) *H. jenkinsii* CSIRO CA3947, e) *H. oxyrhyncha* ZRC 42984, f) *H. signifer* ZRC 42547, g) *H. toshi* CSIRO H5205.01, h) *H. uarnak* CSIRO H5482.01, i) *H. undulata* CSIRO H5483.02, j) *H. walga* MTUF 29999, k) *H.* sp. A CSIRO H5478.01, l) *H.* sp. E CSIRO H5155.01, m) *H.* sp. F CSIRO H5472.01, n) *H.* sp. G MTUF 30001, o) *D. kuhlii* CSIRO H4926.01, p) *D. leylandii* CSIRO H3332.02, q) *D. zugei* CSIRO H4426.07, r) *D. violacea* CSIRO H311. Bars 10 mm. ang: angular cartilage, hyo: hyomandibular cartilage (omitted in some species), ltb: lower tooth band, man: mandibular cartilage, pal: palatoquadrate cartilage, utb: upper tooth band. Numbers in parentheses represent character and character states.



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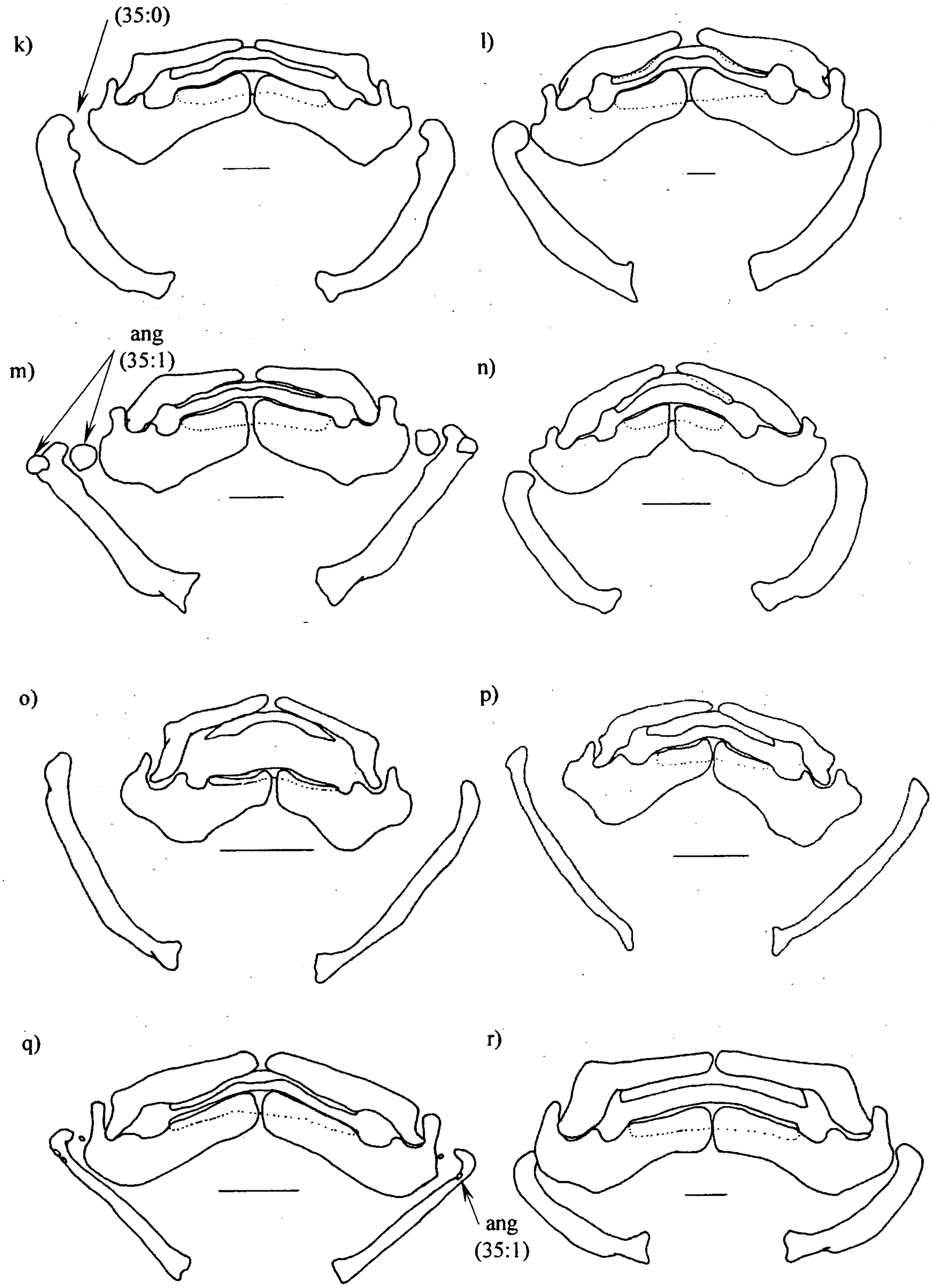
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The thickness of the mandibular arch and the presence or absence of processes on the arch has been variably coded by Nishida (1990), McEachran *et al.* (1996) and Rosenberger (2001a). Among the taxa examined, the mandibular arch is not expanded near the symphysis (Nishida 1990: character 92; McEachran *et al.* 1996: character 33), the anteromedial portion of the palatoquadrate is straight and not anteriorly curved (Rosenberger 2001a: character 17), and an anteromedial process on the mandibular cartilage (Rosenberger 2001a: character 20) is absent or only weakly present (Figure 3.2.9). Lateral (Rosenberger 2001a: character 19) or ventrolateral processes (Nishida 1996) were not observed on the mandibular arch.

The ligament connecting the hyomandibular cartilages to the mandibular cartilage (McEachran *et al.* 1996: character 36) is variable in length. It appears longest in *D. kuhlii* and *D. leylandii* (Figure 3.2.9o-p; Nishida 1990: figure 20F), and somewhat intermediate between the shortest and longest in *H. imbricata* and *H.* sp. F (Figure 3.2.9c,m). However, because of the variable degree of length which poses a difficulty for coding, this character is not included in the present analysis.

Externally on the ligament, a pair of small partly calcified, rod-like cartilage (termed the hyomandibular accessory cartilage 2, HAC2) supported by connecting tissue is reportedly present in several *Dasyatis* species, including *Himantura* (Nishida 1990: character 73). Another pair of small rod-like cartilage (hyomandibular accessory cartilage 1) is reported in groups other than dasyatid stingrays (Nishida 1990: character 94; Lovejoy 1996: character 11). However, as Lovejoy (1996) pointed out, these accessory cartilages are not evident in radiographs. Therefore, the presence of the HAC2 in the Indo-Pacific *Himantura* (Nishida 1990) is treated as uncertain until more specimens become available for clearing and staining.

Embedded in the ligament of several species are two or more pairs of angular cartilages that are readily observed in radiographs. These were observed in *H.* sp. F (Figure 3.2.9m), *D. zugei* (Figure 3.2.9q), *P. sephen, P.* sp., *H. pacifica* and *H. schmardae*. These are either present or absent in *H. imbricata* (Figure 3.2.9c, angulars not shown), *H. pastinacoides* and *H. walga* (Figure 3.2.9j). The angular cartilages in *D. zugei* evident in the radiographs of two specimens examined in this study, are apparently polymorphic, these are absent based on Garman's (1913: plate 71) illustration.

The position of the angular cartilages within the ligament and whether these articulate directly with the mandibular and hyomandibular cartilages have raised a question of their functional role(s) and hence, their homology (Lovejoy 1996). Lovejoy hypothesized that in amphi-American *Himantura* and in several potamotrygonids, these angulars function to strengthen the hyomandibular-mandibular connection based on the anterior-posterior arrangement of one or more cartilage. A second hypothesis proposed by Lovejoy is that the larger angulars observed in *Urolophus cruciatus* (a stingaree) and in several pelagic species (myliobatoids) are a separate derived character. According to Lovejoy, the angulars in the latter may have a shared functional role with the anteromedial aspect of the hyomandibular, based on the attachment of the coracomandibularis on both the hyomandibular and the separate (angular) cartilage, and the direct or ligamentous connection of the hyomandibular to the mandibular.

McEachran *et al.* (1996) followed Lovejoy (1996) in treating the angulars in the amphi-American *Himantura* (including potamotrygonids) and in *Urolophus* (including the pelagic myliobatoids) as separate derived characters, adding that the latter did not possess an elongated ligament connecting the hyomandibular and mandibular cartilages. On the other hand, McEachran *et al.* (1996: figure 8B, character 37) treated the presence of angular cartilage in *Zanobatus schoenleinii* as homologous to that in amphi-American *Himantura* and potamotrygonids, coding it as a third character state based on its posterior position in the ligament, although the ligament is not elongated in this species.

The angular cartilages in *H.* sp. F appears robust, as those seen in *Urolophus cruciatus* by Lovejoy (1996: figure 6I), and in *Myliobatis* spp., *Aetomylaeus maculatus, Aetobatus narinari, Rhinoptera jussieui* and *Mobula hypostoma* (Garman 1913: plates 73-74), and are not directly articulated to the mandibular or hyomandibular (Figure 3.2.9m). On the other hand, the angular cartilages in the other taxa observed in this study, are smaller, rather more granular in size and appear scattered within the matrix of connective tissue.

Two pairs of angular cartilages on each side of the mandibular arch of *H.* sp. F as observed from the radiographs, are arranged in a horizontal position rather than in a vertical position. Furthermore, it is noted that the mouth of *H.* sp. F is extremely tubular (Figure 5.3.14b). Therefore, the angular cartilages in this and other species are most likely to assume both functional roles in strengthening the hyomandibular - mandibular connection, as well as a shared role with the anteromedial aspect of the hyomandibular, i.e. providing support to the mandibular arch. Thus, the vertical position of the angulars is likely to represent a variation of a homologous character. As stated by Lovejoy (1996), the treatment of the angular cartilages in the *Urolophus* and pelagic stingrays as being a separate character from the amphi-American *Himantura* and potamotrygonids, is tentative, pending further research on the branchial musculature, particularly the insertion of the spiracularis with respect to the coracomandibularis (McEachran *et al.* 1996).

The hyoid and branchial arches also provide phylogenetically informative characters, i.e. state of the basihyal, whether present or absent, and either segmented or unsegmented (Nishida 1990: character 68; Lovejoy 1996: character 18; McEachran *et al.* 1996: character 39; Rosenberger 2001a: character 22), articulation of the ceratohyal cartilage with the basihyal (McEachran *et al.* 1996: character 40), and shape of the anterior margin of the medial basibranchial plate (Rosenberger 2001a: character 21). However, these structures were not investigated intensively in this study, and they are not readily evident in radiographs. Therefore characters regarding the hyoid and branchial arches were not considered until more specimens become available for clearing and staining.

35. *Angular cartilage (enlarged or minute) between mandibular and hyomandibular cartilages* (modified from Nishida 1990: character 75; Lovejoy 1996: characters 12 & 13; McEachran *et al.* 1996: characters 37 & 38). — Absent, coded as state 0 (Figure 3.2.9a-d,f-i,k-l,n-p,r) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. oxyrhyncha, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-E, *H.* sp. G, *D. leylandii, D. violacea*); present, coded as state 1 (Figure 3.2.9m) (*H.* sp. F, *P. sephen, P.* sp., *H. pacifica, H. schmardae*). Polymorphic states were coded for *H. imbricata, H.*

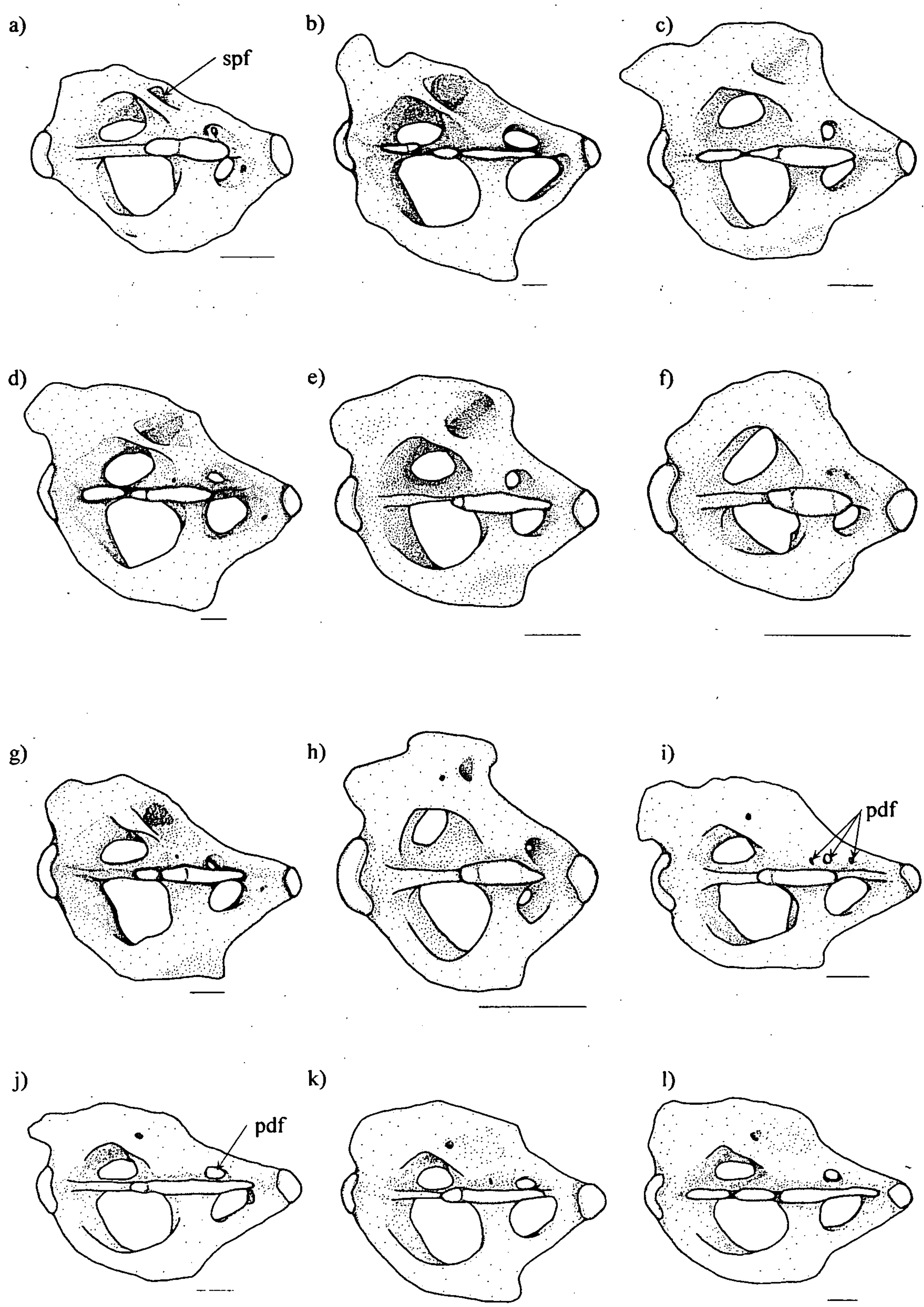
pastinacoides, *H. walga* (Figure 3.2.9j), *D. kuhlii* and *D. zugei* (Figure 3.2.9q). Unknown state coded for *D. acutirostra*, and *D. laosensis*.

Scapulocoracoid (Figures 2.1.6, 3.2.10) *and pectoral-fin*

The scapulocoracoid consists of several fused elements, i.e. a medial coracoid bar lying across the long axis of the body and fused to a dorsolateral scapular process, and a suprascapular cartilage that is fused to the first synarcual (McEachran *et al.* 1996: character 41). Laterally, the scapulocoracoid articulates with elements of the pectoral-fin comprising the propterygium, mesopterygium and metapterygium through respective pro-, meso- and meta-condyles (Figures 2.1.6, 3.2.10). These condyles are all observed to be horizontally arranged (McEachran *et al.* 1996: character 47), the mesocondyle variable in number and shape, and variably positioned between the procondyle and the mesocondyle (McEachran *et al.* 1996: character 48).

The anterior end of the pectoral propterygium of the Indo-Pacific *Himantura* and other discoid rays invariably articulates with the antorbital cartilage (Lovejoy 1996; McEachran *et al.* 1996: character 49), and extends to the snout apex. The first segmentation of the propterygium (Lovejoy 1996: character 25; Rosenberger 2001a: character 25) is variable among species, although all pectoral-fins were observed to be plesodic (McEachran *et al.* 1996: characters 52 & 53) and the radials not distally expanded (Nishida 1990: character 82) to articulate with neighbouring radials. Segmentation of the pectoral-fin radial of the mesopterygial section in *H.* sp. G (MTUF 30001) is unique among other Indo-Pacific *Himantura* in that smaller segments between larger ones are present. However, this observation was based on the single specimen available for this species. The distal end of the propterygium in all taxa extends beyond the procondyle in all taxa examined (Lovejoy 1996: character 26; McEachran *et al.* 1996: character 51). Radials on the rostral extension of the propterygia are also present in all taxa examined (Nishida 1990: character 70).

Figure 3.2.10. Left scapulocoracoids (lateral view). a) *H. chaophraya* CSIRO H5283.01, b) *H. gerrardi* CSIRO H5284.04, c) *H. jenkinsii* CSIRO H3622.01, d) *H. jenkinsii* CSIRO H4004.05, e) *H. jenkinsii* CSIRO H5475.01, f) *H. oxyrhyncha* ZRC 42984, g) *H. pastinacoides* CSIRO H5479.02, h) *H. signifer* ZRC 42547, i) *H. toshi* CSIRO H5206.01, j) *H. toshi* CSIRO H5586.01, k) *H. toshi* CSIRO H5586.03, l) *H. toshi* CSIRO H5586.04, m) *H. toshi* CSIRO H5587.01, n) *H. toshi* CSIRO H5588.01, o) *H. toshi* CSIRO H5589.01, p) *H. uarnacoides* CSIRO H5470.01, q) *H. undulata* CSIRO H5481.01, r) *H. walga* CSIRO H5474.02, s) *H.* sp. A CSIRO H5478.01, t) *H.* sp. E CSIRO H4916.01, u) *H.* sp. F CSIRO H5472.01, v) *H. fai* CSIRO H5480.01, w) *H. granulata* CSIRO CA1255, x) *P. sephen* CSIRO H5479.20. Bars 10 mm. pdf: postdorsal fenestra, spf: scapular process fenestra.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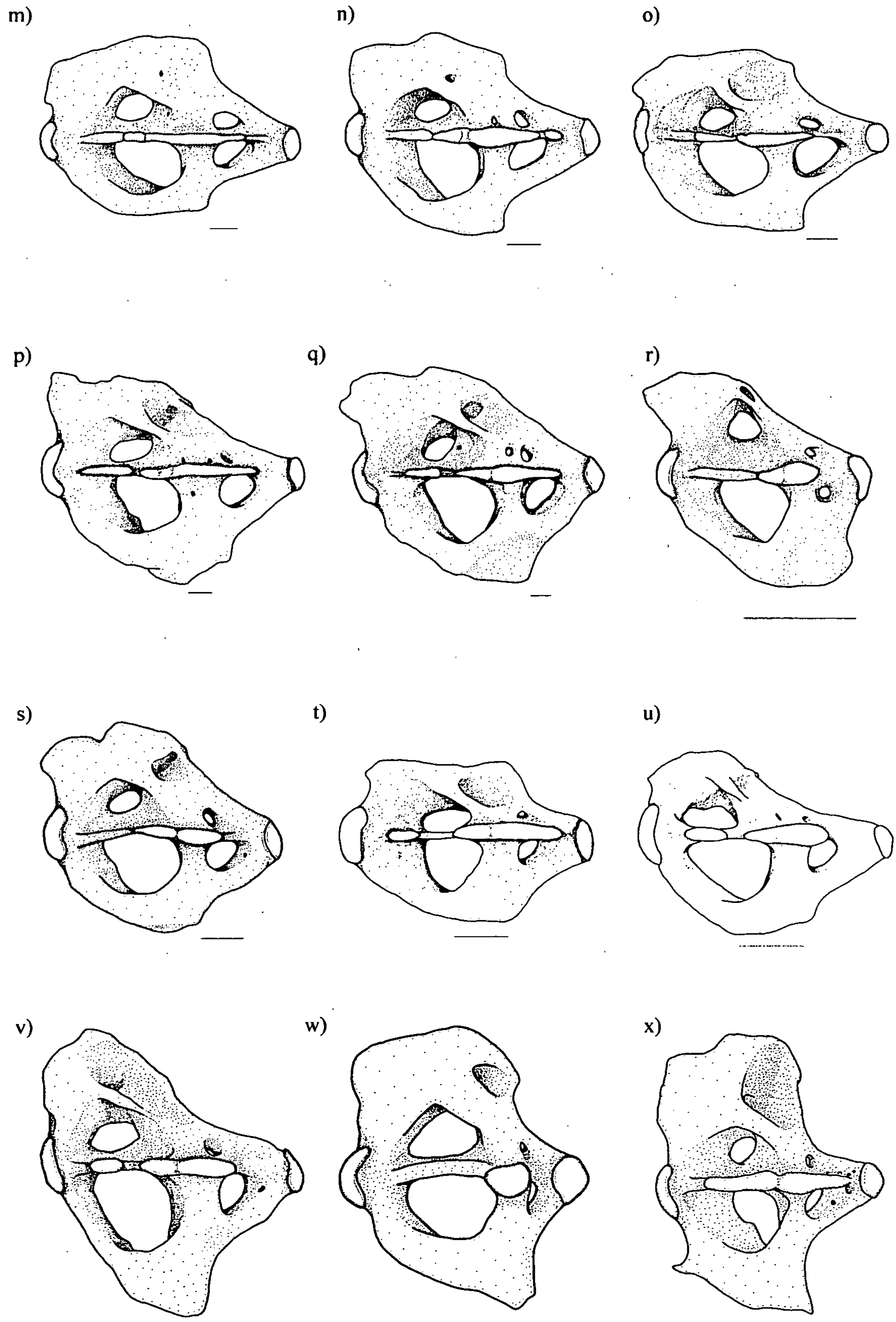
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All taxa examined, except *D. zugei*, possess a single mesopterygium (Lovejoy 1996: character 27). In *D. zugei*, two or three mesopterygia on each side are usually present. The mesopterygium varies in width and length, thus is not included in the character matrix due to difficulty with character coding. A neopterygial 'space' on the lateral ridge of the scapulocoracoid where the mesopterygium base does not extend (McEachran *et al.* 1996: character 48), is absent in all the ingroup taxa examined.

The metapterygium is laterally arched posteriorly, and may be anterolaterally extended beyond the metacondyle. When such an extension is present, radials may articulate from it. The distal tip of the metapterygium is also segmented, as with the propterygium. Rosenberger (2001a: character 27) coded the character state of the segmentation of the metapterygium based on the number of segments. However, this character was not included in the present study because it is a continuous character.

The lateral face of the stingray scapulocoracoid is variable in shape among the ingroup and outgroup species (Figure 3.2.10). Nishida (1990) encountered difficulty in coding a character state regarding such variations, and found the character as not suitable for phylogenetic analyses. However, McEachran *et al.* (1996: character 45) focused on the length of the scapular process, and coded the character based on its length and shape, i.e. whether short and straight or long and posteriorly displaced. In this study, this character was modified to consider whether the elongated scapular process and expanded surface ventral to the condyles result in the scapulocoracoid height being equal to or shorter than its width, or taller than wide.

The fenestrae on the lateral surface of the scapulocoracoid of the taxa examined comprised of an anterodorsal, anteroventral, postdorsal and postventral component. However, among these, the number and size of the postdorsal fenestra is most variable, varying between one to five fenestrae, and the size ranging from minute to moderately large. Intraspecific variation on the number of postdorsal fenestrae was also observed in at least two species, *H. jenkinsii* (Figure 3.2.10c-e) and *H. toshi*

(Figure 3.2.10i–o), as is reported in other stingray species (e.g. *Dasyatis akajei* and *Myliobatis tobijei* by Nishida (1990), and *Urotrygon rogersi* and *Urobatis jamaicensis* by Lovejoy (1996)). The presence of a fenestra on the scapular process (Nishida 1990: character 72; Lovejoy 1996: character 23; McEachran *et al.* 1996: character 46) was observed in all except in *H. oxyrhyncha* (Figure 3.2.10f). However, this character was not included in the analysis because it is autapomorphic in this species. The scapular process fenestra is also observed in *H. signifer*, although it was not mentioned by Compagno and Roberts (1982), and appears absent in their illustration. In fact, the postdorsal fenestra of this species as observed in this study and that illustrated by Compagno and Roberts (1982: figure 9A) also differ in number.

The scapular process fenestra if present, is observed to have varying degrees of connection with the anterodorsal fenestra. As explained in Chapter 2, the inside wall connecting the fenestra of the scapular process to the anterodorsal fenestra is shaped like a twisted 'S'. On the dorsolateral surface of the scapular process, a groove resulting from the connection with the anterodorsal fenestra displays varying depths among species, or may be entirely absent, so that the scapular process fenestra appears as a simple opening on the surface. According to Nishida (1990), 'the anterodorsal fenestrae tend to be more complicated in myliobatoids,' in which he probably meant the rather complicated connection with the scapular process fenestra.

36. *First segmentation of the propterygium* (modified from Lovejoy 1996: character 25). — Along nasal capsule, coded as state 0 (*H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-D, *H.* sp. F-G, *D. kuhlii, D. leylandii, P. sephen, H. pacifica, H. schmardae*); at or anterior of nasal capsule, coded as state 1 (*H.* sp. E, *D. violacea, D. zugei*). Both states were observed in *H. chaophraya*, so this character was coded as polymorphic for this taxon. Unknown state for *D. acutirostra, D. laosensis,* and *Pastinachus* sp.

37. *Scapulocoracoid height in lateral face* (modified from McEachran *et al.* 1996: character 45). — Equal to or shorter than wide, coded as state 0 (Figure 3.2.10a-u) (*H. chaophraya, H. gerrardi*[a], *H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A, *H.* sp. E-F, *D. kuhlii, D. leylandii, D. zugei*); taller than wide, coded as state 1 (Figure 3.2.10v-x) (*H. fai, H. granulata, D. violacea, P. sephen, P.* sp.). Unknown state for *H. gerrardi*[b], *H. imbricata, H.* sp. B-D, *H.* sp. G, *D. acutirostra, D. laosensis, H. pacifica,* and *H. schmardae.*

Pelvic girdle (Figures 2.1.7, 3.2.11)

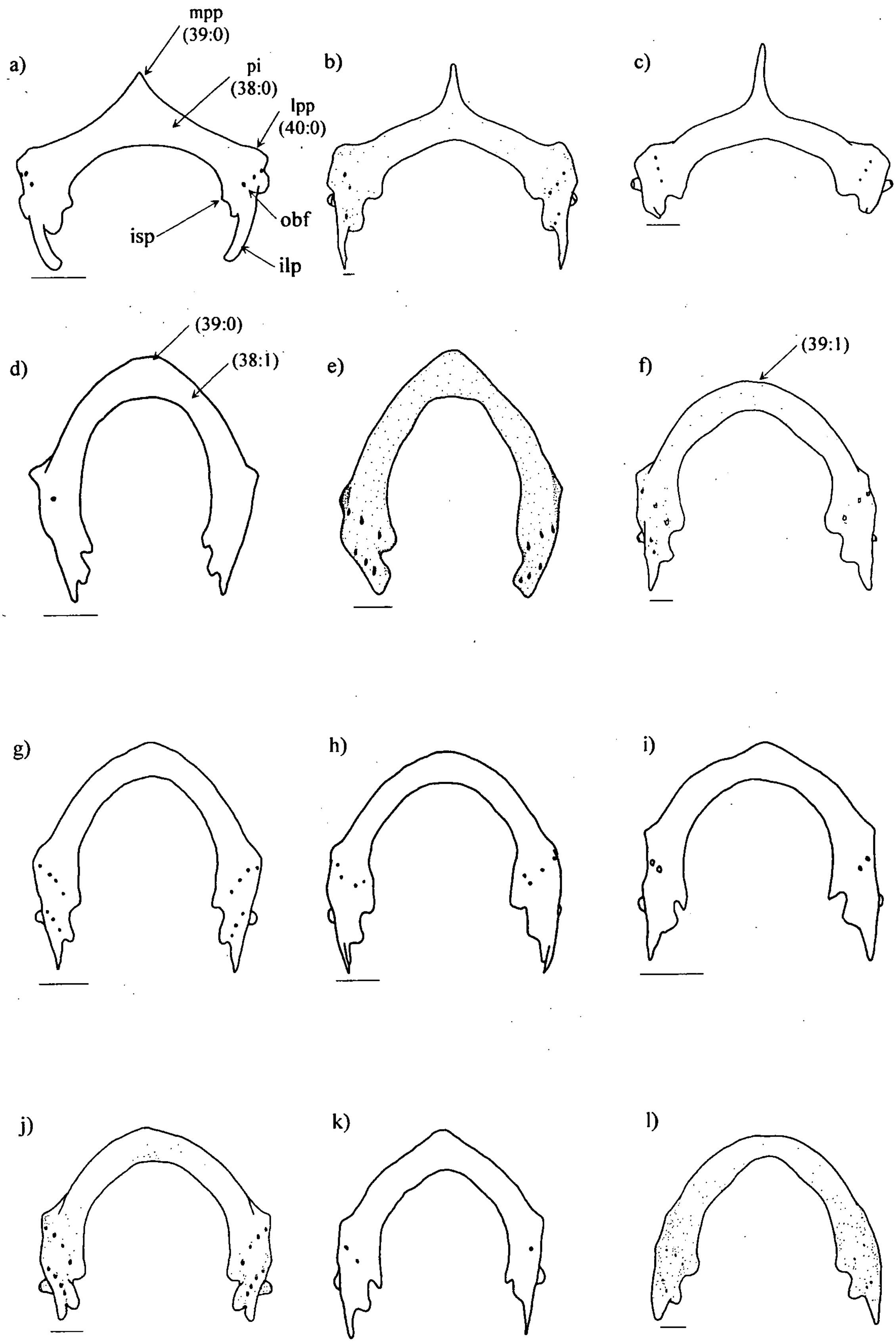
The pelvic girdle consists of a puboischiadic bar with several lateral and/ or a medial prepelvic processes. The bar is usually anteriorly arched (Lovejoy 1996: character 30; McEachran *et al.* 1996: character 54; Rosenberger 2001a: character 29 & 30), more or less depressed medially, and laterally thickened with several obturator foramina present on the lateral segment. On the posterolateral end of the bar are two condyles for articulation with the basipterygium and pelvic propterygium.

A well-developed median triangular prepelvic process (Nishida 1990: character 88; Lovejoy 1996: character 29; McEachran *et al.* 1996: character 55; Rosenberger 2001a: character 28) is observed in several non-Indo-Pacific *Himantura* species (Figure 3.2.11a-c). The anterior margin of the puboischiadic bar with such process is concave and appears angularly arched. On the other hand, when the process is absent or only weakly present, the anterior margin of the bar is convex, and the pelvic girdle appears broadly arched, as observed in all the Indo-Pacific *Himantura* species (Figure 3.2.11d-v), *D. zugei* and *D. violacea.*

The anterolateral prepelvic processes are unique in *H.* sp. F (Figure 3.2.11u) among all the other Indo-Pacific *Himantura*, in that it is spatula-like and its length is about the width of the arched puboischiadic bar. The process is also conspicuous in three *Dasyatis* species, although not as elongated.

On the posterolateral segment of the puboischiadic bar, are two other lateral processes, i.e. the iliac and ischial processes. The iliac process on the tip of the bar is strongly compressed and dorsoposteriorly curved, whilst the ischial process on the inner margin of the bar below the iliac process appear as a small rounded knob. Both processes are present in all the taxa examined, with varying degrees of development. The iliac processes of *D. kuhlii* and *P. sephen* are notably elongated (Figure 3.2.11a-b), however initial investigations of this character in the former species suggests the length may be sexually dimorphic. Following Nishida (1990), this character was considered not phylogenetically informative due to difficulty with coding.

Figure 3.2.11. Pelvic girdles (dorsal view). a) *D. kuhlii* CSIRO CA4307, b) *P. sephen* CSIRO H5479.20, c) *P.* sp. CSIRO H5472.04, d) *H. chaophraya* CSIRO H5283.01, e) *H. fai* CSIRO H5480.01, f) *H. gerrardi* CSIRO H5284.04, g) *H. granulata* AMS I9673, h) *H. jenkinsii* CSIRO H3622.01, i) *H. oxyrhyncha* ZRC 42984, j) *H. pastinacoides* CSIRO H5479.02, k) *H. signifer* ZRC 42547, l) *H. toshi* CSIRO H1041.02, m) *H. toshi* CSIRO H5205.01, n) *H. toshi* CSIRO H5586.04, o) *H. uarnacoides* CSIRO H5470.01, p) *H. undulata* CSIRO H5481.01, q) *H. walga* CSIRO H5474.02, r) *H.* sp. A CSIRO H5284.05, s) *H.* sp. A CSIRO H5479.08, t) *H.* sp. E CSIRO H4916.01, u) *H.* sp. F CSIRO H5472.01, v) *H.* sp. G MTUF 30001. Bars 10 mm. ilp: iliac process, isp: ischial process, lpp: lateral prepelvic process, mpp: medial prepelvic process, obf: obturator foramen, pi: puboischiadic bar. Numbers in parentheses represent character and character state.


a)
mpp
(39:0)
pi
(38:0)
lpp
(40:0)
obf
isp
ilp
b)
c)
d)
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(38:1)
e)
f)
(39:1)
g)
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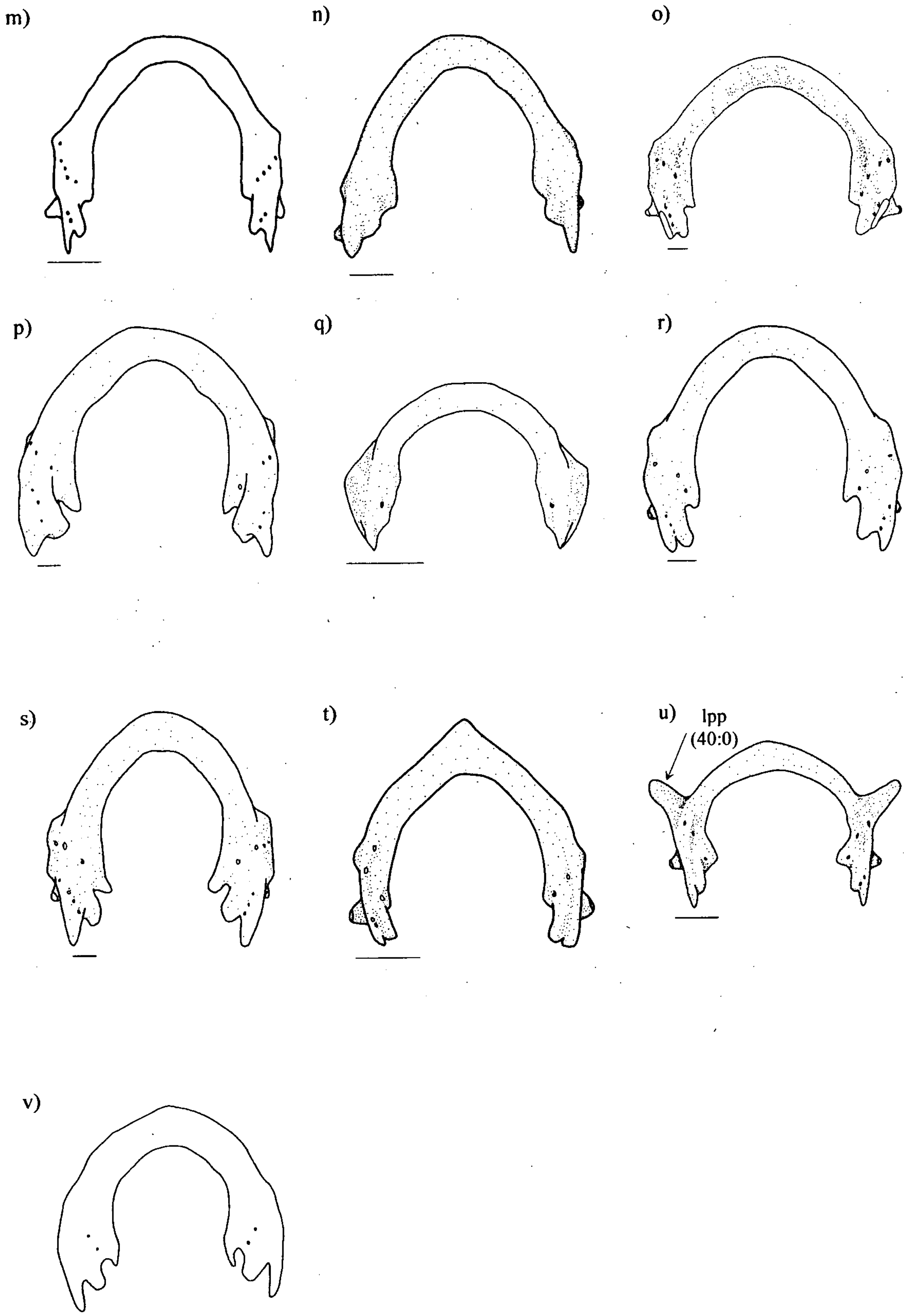
m)
n)
o)
p)
q)
r)
s)
t)
u)
lpp
(40:0)
v)

38. *Puboischiadic bar*. — Angularly arched, coded as state 0 (Figure 3.2.11a-c) (*D. kuhlii, D. leylandii, P. sephen, P.* sp., *H. pacifica, H. schmardae*); not angularly arched, coded as state 1 (Figure 3.2.11d-v) (all Indo-Pacific *Himantura, D. violacea, D. zugei*). Unknown state for *D. acutirostra,* and *D. laosensis.*

39. *Median prepelvic process* (modified from Nishida 1990: characters 77 & 88; McEachran *et al.* 1996: 55). — Present, coded as state 0 (Figure 3.2.11a-e,i,k,t,v) (*H. chaophraya, H. fai, H. oxyrhyncha, H. signifer, H.* sp. E, *D. kuhlii, D. leylandii, D. violacea, P. sephen, P.* sp., *H. pacifica, H. schmardae*); absent, coded as state 1 (Figure 3.2.11f-h,j,l-s,u) (*H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-D, *H.* sp. F-G, *D. zugei*). Unknown state for *D. acutirostra,* and *D. laosensis.*

40. *Anterolateral processes*. — Present, coded as state 0 (Figure 3.2.11a,u) (*H.* sp. F, *D. kuhlii, D. leylandii, D. violacea*); absent, coded as state 1 (Figure 3.2.11b-t,v) (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. A-E, *H.* sp. G, *D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*). Unknown state for *D. acutirostra,* and *D. laosensis.*

Pelvic-fin and mixopterygium (Figures 2.1.8, 3.2.12)

The pelvic-fin skeleton consists of two basal cartilages, i.e. the basipterygium and pelvic propterygium, and the pelvic radials. The basipterygium is comparable to the metapterygium of the pectoral-fin and is sometimes termed the pelvic metapterygium (e.g. Nishida 1990: figure 37). The pelvic propterygium represents a fusion of the basal part of the pelvic radials, which from its distal part the radials extend freely. The distal half of each radial is segmented into three or four small segments, and the distal tip is usually bifurcated to form a largely plesodic pelvic-fin. In males, the posterior pelvic radials are also fused and modified to form the clasper whose base is connected to the distal tip of the basipterygium. Thus the number of pelvic radials in males is always fewer than in females of the same species (Nishida 1990: table 3). The basal segments connecting the mixopterygium, i.e. the skeletal components of the clasper, to the distal tip of the basipterygium are relatively short, and variable in number among species (Figure 2.1.8, 3.2.12). The basals are supported by a longitudinal cartilage, which in the Indo-Pacific *Himantura* may or may not merge with the axial cartilage (Figure 3.2.12c-h, j-m).

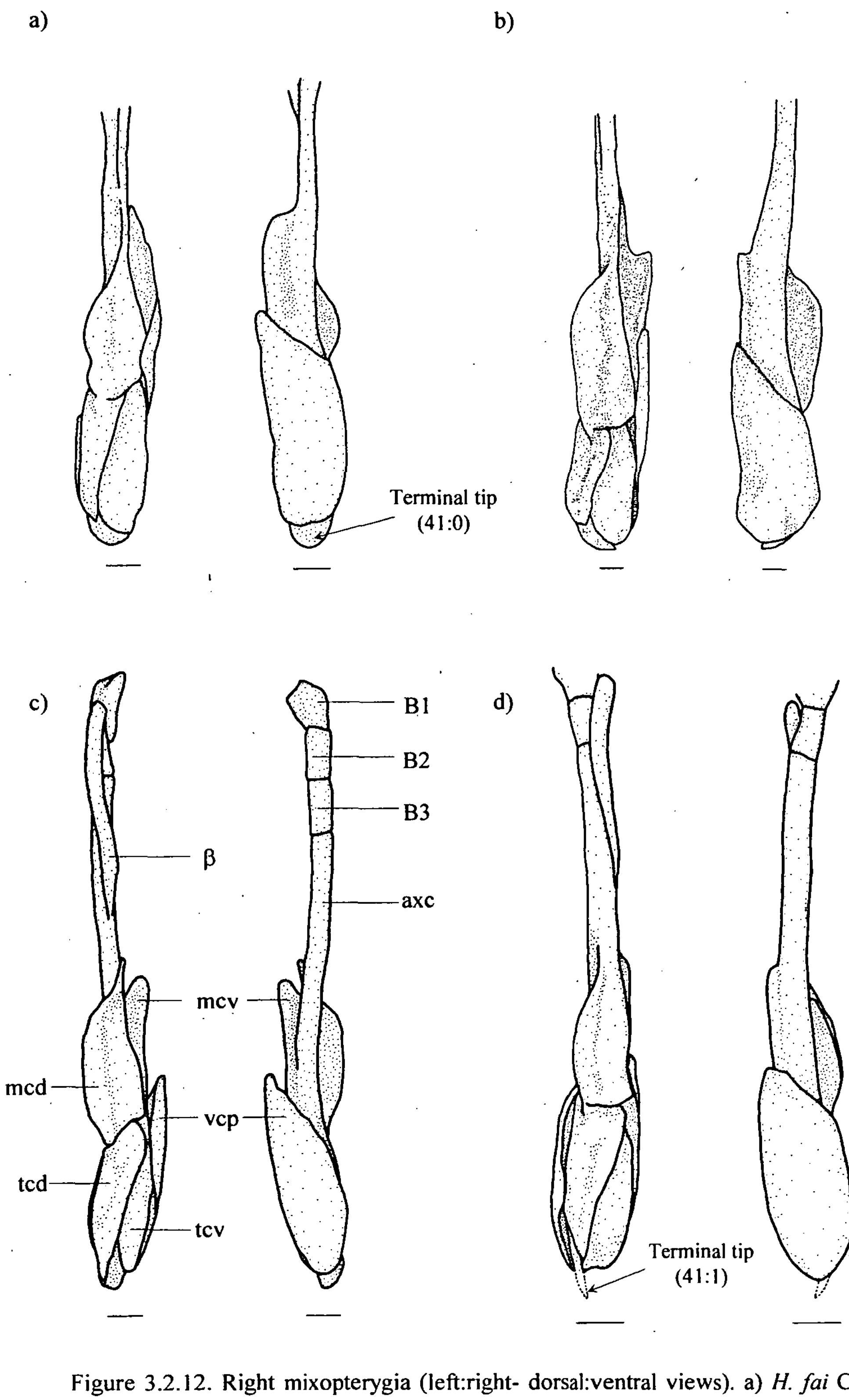

Figure 3.2.12. Right mixopterygia (left:right- dorsal:ventral views). a) *H. fai* CSIRO H4426.33, b) *H. granulata* CSIRO H4426.32, c) *H.* sp. A CSIRO H3903.02, d) *H. jenkinsii* CSIRO H4004.04. Bars 10 mm. axc: axial cartilage, B1-3: basal segment 1-3, β: beta cartilage, mcd: dorsal marginal cartilage, mcv: ventral marginal cartilage, tcd: dorsal terminal cartilage, tcv: ventral terminal cartilage, vcp: ventral covering piece. Numbers in parentheses represent character and character state.

continued...

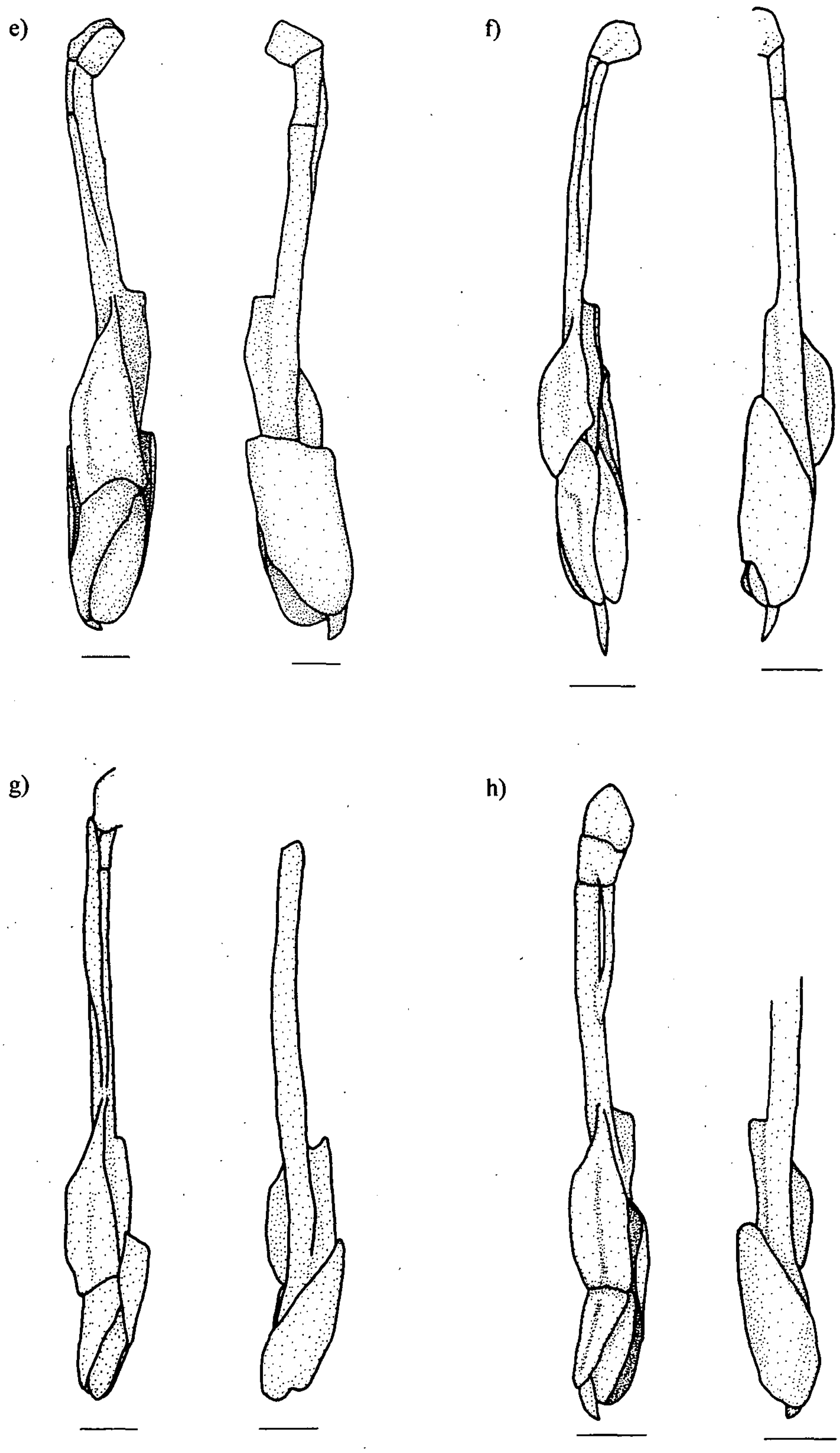

Figure 3.2.12. Continued. e) *H. jenkinsii* CSIRO H5585.01; f) *H. pastinacoides* CSIRO H5479.02; g) *H. toshi* CSIRO H1041.02; h) *H. toshi* CSIRO H5586.04. Bars 10 mm.

continued...

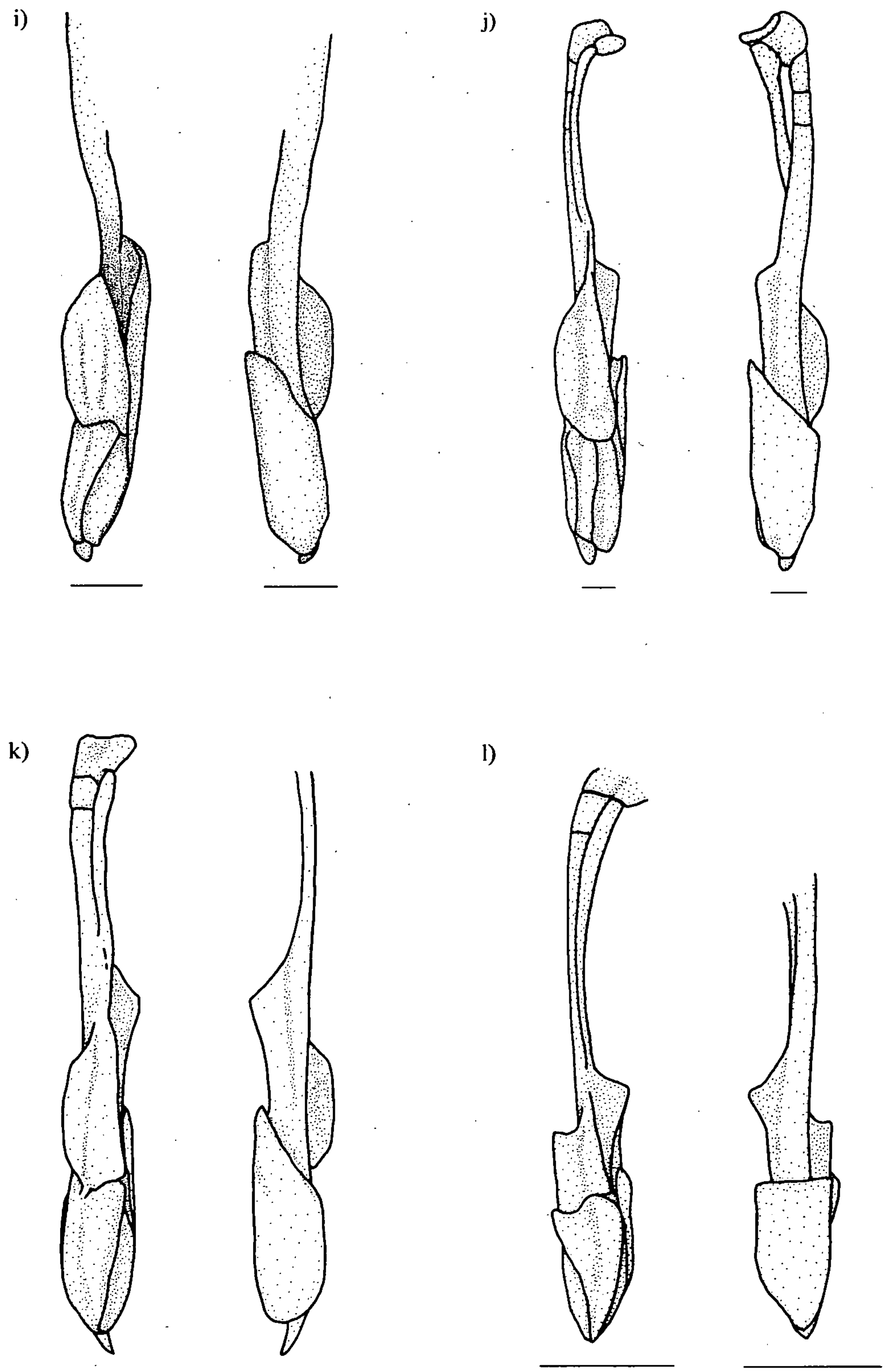

Figure 3.2.12. Continued. i) *H. toshi* CSIRO H5588.01, j) *H. uarnak* CSIRO H5476.03, k) *H. undulata* CSIRO H5481.01, l) *H. walga* CSIRO H5474.01. Bars 10 mm.

continued...

m)

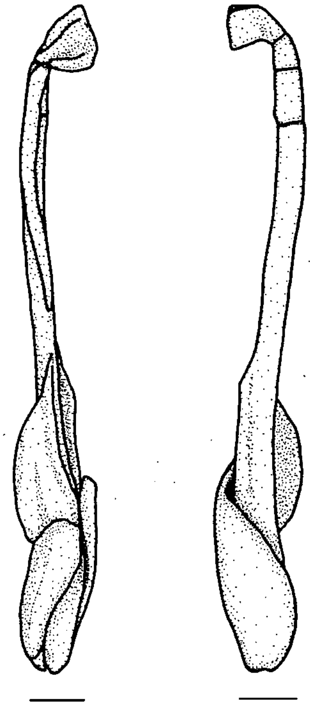

Figure 3.2.12. Continued. m) *H.* sp. E CSIRO H5155.01. Bars 10 mm.

The axial cartilage, which is the main axis of the mixopterygium, assumes different degrees of complexity in its distal part. However, each possess a dorsal and ventral marginal cartilage, a dorsal and ventral terminal cartilage, and a shield-like ventral cartilage termed the ventral covering piece (Figure 3.2.12). The terminal tip varies from 'tapering, elongate and pointed' to 'short, flat and spatula-like'.

41. *Shape, terminal tip of axial cartilage.* — Short spatula-like, coded as state 0 (Figure 3.2.12a-c) (*H. fai, H. granulata, H.* sp. A); elongated, tip pointed, coded as state 1 (Figure 3.2.12d-m) (*H. jenkinsii, H. pastinacoides, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H. walga, H.* sp. E, *D. kuhlii, D. leylandii, P. sephen, P.* sp.). Unknown state for *H. chaophraya, H. gerrardi, H. imbricata, H. oxyrhyncha, H.* sp. B-D, *H.* sp. F-G, *D. acutirostra, D. laosensis, D. violacea, D. zugei, H. pacifica,* and *H. schmardae*.

Vertebrae

The vertebrae of the Indo-Pacific *Himantura* consist of a first synarcual, intersynarcual vertebrae, second synarcual (McEachran *et al.* 1996: character 43), monospondylous vertebrae, diplospondylous vertebrae and an unsegmented notochordal sheath on the tail.

The first synarcual articulates anteriorly with the neurocranium by an odontoid process and two occipital condyles. Posteriorly, the lateral surface of the fused suprascapular has a large facet to accommodate a unique ball and socket type of articulation with the scapular process of the scapulocoracoid (McEachran *et al.* 1996: character 42). Lovejoy (1996) coded several character states of the first synarcual, which included its width *vs* its height, and aspects regarding the lateral stay, i.e. the position of its base relative to the spinal nerve foramina, its presence or absence, and the degree of its projection. However, based on Lovejoy's work, these characters may only be useful for higher systematic studies, as the characters apparently are invariable between the amphi-American *Himantura*, *Himantura jenkinsii*, and *Dasyatis* spp. Consequently, these characters were not included in this study. However, also due to a lack of foresight, such data were not documented when dissections were carried out to extract other skeletal parts.

Diplospondylous tail vertebrae are detected in radiographs by a change in size between two adjacent vertebrae at a position just posterior of the pelvic girdle. The diplospondylous tail vertebrae of Indo-Pacific *Himantura* usually extend to the region around the base of the sting, beyond which is an unsegmented, cartilaginous rod. A pattern was observed that in several species the vertebrae actually terminate before the sting base, while in others, these extend further beyond the sting.

Apart from the presence of a stinging spine(s) on the tail, appendages, specifically the dorsal fin (Nishida 1990: character 42; Lovejoy 1996: character 32), and cartilaginous dorsal and ventral skin fold (Nishida 1990: characters 56, 79 & 80; Lovejoy 1996: character 33; McEachran *et al.* 1996: character 56) are lacking in the Indo-Pacific *Himantura*.

42. *Diplospondylous vertebrae* (modified from Lovejoy 1996: character 31; McEachran *et al.* 1996: character 56; Rosenberger 2001a: character 32). — Extended to or slightly beyond sting base (0-10 centra), coded as state 0 (*H. granulata, H. imbricata ,H. oxyrhyncha, H. signifer, H. walga, H.* sp. G, *D. kuhlii, D. leylandii, D. violacea, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*); not extended to sting base, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. jenkinsii, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-E). Unknown state for *H.* sp. F, *D. acutirostra,* and *D. laosensis*.

43. *Cartilaginous radials of caudal fin or caudal folds.* — Present or only as remnants, coded as state 0 (*D. kuhlii, D. violacea*); absent (caudal fin and/or fold entirely absent), coded as state 1 (all Indo-Pacific *Himantura*, except *H.* sp. F, *D. acutirostra, D. laosensis, D. leylandii, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*). Unknown state for *H.* sp. F.

Musculature

Cephalic and branchial musculature patterns were both included in the character matrix for phylogenetic analysis by Nishida (1990), Lovejoy (1996) and McEachran *et al.* (1996). However, in these studies, many of the observed patterns were found to be either too variable for coding, or that the phylogenetic significance of a character was considered as equal to those based on the skeletal character. For example, the number of dorsal constrictors is directly associated with the number of brachial arches, and the cephalic-fin muscles are related to the skeletal development of the cephalic-fin (Nishida 1990). Both of these characters however, are irrelevant in the present study.

Nishida (1990) demonstrated that aspects of the ventral musculature were more useful for character coding, compared with the dorsal musculature. Only a single dorsal character, i.e. origin of the dorsal longitudinal bundles from the neurocranium was found to be phylogenetically informative in Nishida's study. In a separate work (McEachran *et al.* 1996) however, with the inclusion of several additional taxa (not used by Nishida), the presence or absence of the ethmoideo-parethmoidalis becomes the only phylogenetically informative dorsal character. On the other hand, depending on the taxa involved in the respective studies, ventral characters included several or all of the following characters: presence or absence of a tendon between the depressor rostri muscle and its insertion point, extension of the spiracuralis, posteromedial extension of the adductor mandibulae, presence or absence of the intermandibularis posterior, medial fusion of the intermandibularis posterior, and the medial fusion of the coraco-hyoideus.

Among these characters, only the development of the spiracularis is variable among the dasyatid genera (Lovejoy 1996; McEachran *et al.* 1996). This muscle originates on the otic region of the neurocranium, extends ventrally along the prespiracular wall and variably inserts on the hyomandibular or the posterior surface of the mandibular cartilage. Muscle pattern characteristics were not included in the present study however, as these patterns, particularly sections of the the ventral cranial, were not investigated and not documented during dissections carried out to extract skeletal parts. In hindsight, observations of the muscular insertions could be a useful character in the dasyatids.

3.2.1.3 Biology and Physiology

Colour

Colour and colour pattern characters were investigated by Rosa (1985) in his phylogenetic studies of the potamotrygonids. However, Rosa concluded the phylogenetic significance of these characters holds little importance at the generic level. Other workers too, have not utilised colour characters (Nishida 1990; Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a). Perhaps this is due to the fact that the colour of batoids are usually in shades of muted colours (e.g. see Kemp 1999), and that colour patterns when present, usually indicate intraspecific variation (e.g. Rosa 1985). Furthermore, as Rosa noted, temporal changes of individual colour patterns are present in two batoid species, i.e. *Rhinobatos percellens* and *Potamotrygon motoro*. Such changes have not yet been recorded in species of dasyatids however, although intraspecific colour variation is common in several Indo-Pacific *Himantura* species (pers. observation this study).

The presence of both ocellate and reticulate patterns of several *Potamotrygon* species was also observed by Rosa (1985). This led him to hypothesize that such colour patterns might represent parallelism. Within the Indo-Pacific *Himantura*, the spotted colour pattern (when present, it is present from birth) may persist into adulthood in several species, while in other species, the spots gradually merge and transform into reticulations as the individual develops with age. Thus, colour pattern itself is not particularly phylogenetically informative. On the other hand, the presence or absence of colour pattern is considered as a phylogenetically informative character. This follows that in many other vertebrate taxa, the colour pattern develops ontogenetically, i.e. developing only later in the life stages. The idea that phylogeny could be 'read' from ontogenetic sequence is based upon the

Biogenetic Law which states that ontogeny recapitulates phylogeny (see Kitching *et al.* 1998). A similar phylogenetically informative colour character is the presence or absence of bands on the tail.

44. *Dorsal disc patterning.* — Absent, coded as state 0 (*H. chaophraya, H. fai,H. imbricata, H. jenkinsii, H. pastinacoides, H. signifer, H. uarnacoides, H. walga, H.* sp. B-G, *D. acutirostra, D. laosensis, D. violacea, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*); present, coded as state 1 (*H. gerrardi*[b], *H. oxyrhyncha, H. uarnak, H. undulata, H.* sp. A, *D. kuhlii, D. leylandii*). Both states were observed in *H. gerrardi*[a], *H. granulata,* and *H. toshi,* so this character was coded as polymorphic for these taxa.

45. *Tail banding.* — Present, coded as state 0 (*H. gerrardi, H. toshi, H. uarnak, H. undulata, H.* sp. A, *H.* sp. C, *D. kuhlii, D. leylandii*); absent, coded as state 1 (*H. chaophraya, H. fai, H. granulata, H. imbricata, H. jenkinsii, H. oxyrhyncha, H. pastinacoides, H. signifer, H. uarnacoides, H. walga, H.* sp. D-G, *D. acutirostra, D. laosensis, D. violacea, D. zugei, P. sephen, P.* sp., *H. pacifica, H. schmardae*). Polymorphic character state coded for *H.* sp. B.

Sexual dimorphism

Sexually dimorphic characteristics, apart from the presence of claspers and corresponding fewer number of pelvic-fin radial counts in males, are common in batoids especially in mature individuals. These include the acute and elongated tooth cusps of males, as observed in a number of dasyatid species (e.g. Nishida 1990), and the more angular disc shape of males of several rajoid species (e.g. Last & Stevens 1994). As for *D. violacea* however, acute and elongated tooth cusps are found in both males and females, which Bourdon (2000) suggests is an advantage for its pelagic lifestyle. Among the Indo-Pacific *Himantura*, sexual dental dimorphism was observed in several species, but not in others. Sexual disc shape dimorphism was not observed in any of the Indo-Pacific *Himantura* or other dasyatids.

46. *Sexual dental dimorphism.* — Present, coded as state 0 (*H. imbricata, H. oxyrhyncha, H. signifer, H. walga, H.* sp. G., *D. acutirostra, D. kuhlii, D. laosensis, D. leylandii, D. zugei*); absent, coded as state 1 (*H. chaophraya, H. fai, H. gerrardi, H. granulata, H. jenkinsii, H. pastinacoides, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A-F, *D. violacea*). Unknown state for *P. sephen, P.* sp., *H. pacifica,* and *H. schmardae.*

Habitat

Most of the Indo-Pacific *Himantura* species were recorded only from marine and/or brackishwater environments, and fewer species recorded only from fresh- and brackish- water. The ability of sharks and rays to survive in a range of habitats with varying salinity levels is associated with their ability to retain urea in their blood and body fluids. In this respect, the freshwater potamotrygonids are unique among the rays due to their ability to adapt fully to the freshwater environment by lowering their urea content, and their ability to adjust (increase) urea levels when exposed to salt water (reviewed by Rosa 1985). This unique characteristic of the potamotrygonid is supported by T. Otake (unpublished) in his study on the adaptation of several freshwater Indo-Pacific stingrays (i.e. *Himantura signifer, H. chaophraya, P. sephen* and *D. laosensis*). Based on his studies of the rectal gland weight and morphology, nephron morphology, and analyses of the serum composition (i.e. sodium and chloride concentrations) and statoconium Sr:Ca ratios in these species, Otake concluded the results suggest that the freshwater Indo-Pacific stingrays were not fully adapted for a freshwater environment. This led him to hypothesize a connection between the freshwater and marine environment during the life history of these species.

The character 'urea retention ability' was included in the character matrix of Lovejoy (1996: character 38). However, because data for this character is lacking for most species, this character was not included in the present study.

On the other hand, the character 'habitat distribution', i.e. whether a species is obligate freshwater, brackishwater or marine, is included in the analysis. The information is primarily based on known records from personal observations but also gleaned from the literature.

47. *Habitat distribution.* — obligate freshwater, coded as state 0 (*H. oxyrhyncha, H. signifer, H.* sp. G, *D. laosensis*); brackishwater, coded as state 1 (*H.* sp. E-F, *D. zugei, P.* sp.); marine, coded as state 2 (*H. fai, H. gerrardi, H. jenkinsii, H. uarnak, H. undulata, H.* sp. A-D, *D. acutirostra, D. kuhlii, D. leylandii, D. violacea, H. pacifica, H. schmardae*). Polymorphic states were coded for *H. chaophraya, H. granulata, H. imbricata, H. pastinacoides, H. toshi, H. uarnacoides, H. walga, P. sephen.*

Size

Size at first maturity for several of the Indo-Pacific *Himantura* species is found at both ends of a wide range. For example, males of *H. walga* are mature by 175 mm disc width, whilst in *H. jenkinsii*, mature males are only found at about 900 mm disc width (this study). The maximum size for these species, correspondingly is either 'small' or 'large', in which case, may be categorized as not reaching 1 m in disc width or exceeding 1 m in disc width. However, since size is a continuous character, it was not included in the character matrix of the present study.

3.2.2 Phylogenetic analysis

Phylogenetic analysis of the data matrix (Appendix 3.2.2) of 32 taxa of whip-tailed stingrays and 47 characters (characters and character states listed in Appendix 3.2.1), produced 12 equally most parsimonious trees. The strict consensus tree (Figure 3.2.13) resulted in 166 steps with a consistency index (CI) of 0.39, retention index (RI) of 0.64, and rescaled consistency index (RC) of 0.25.

Based on the tree (Figure 3.2.13), the Indo-Pacific *Himantura* is monophyletic, *Dasyatis* polyphyletic and *Pastinachus* monophyletic. All Indo-Pacific *Himantura* and *Pastinachus sephen* + *P.* sp form a polytomy with species of the *Dasyatis*. The clade including Indo-Pacific *Himantura* and *Pastinachus* spp. (node A) is supported by a single character (20:1, presence of secondary denticle band in sub-adults and adults), a character that is also present in the outgroups, but not in any of the *Dasyatis* species. On the other hand, the separation of Indo-Pacific *Himantura* from *Pastinachus* spp. (node D) is supported by five characters. Two of these characters (14:2, clasper pseudosiphon present on the inner margin of the clasper, and 15:1, clasper pseudorhipidion absent) may be unique among the Indo-Pacific *Himantura*, pending confirmation of the states for missing data (Appendix 3.2.2).

Within Indo-Pacific *Himantura* and *Dasyatis*, several sister species relationships are revealed. Moreover, within the Indo-Pacific *Himantura*, a pattern of species subgrouping may be inferred. These are indicated with I, II and III (Figure 3.2.13), and are provisionally defined herein as the '*uarnak*', '*uarnacoides*', and '*signifer*' complexes respectively. Members of the '*uarnak*' complex consist of terminal taxa, are large species and generally have dorsal disc patterns and/or banded tail (except in *H. fai* and *H. jenkinsii*). On the other hand, the dorsal disc surface of members of the '*uarnacoides*', and '*signifer*' complexes are usually uniformly coloured. The latter forms the basal group, and consists of small-sized taxa (i.e. maximum disc width generally not exceeding 500 mm). The three subgroups, although not supported by bootstrap analysis, the relative position of members of each of these subgroups on the phylogenetic tree nevertheless agrees with the (author's) knowledge of the taxonomy of this group of whip-tailed stingrays.

Prior to the 'final' result shown in Figure 3.2.13, several trial analyses of the data set were carried out, with an aim to test the topologies of two ungrouped taxa within the uarnak complex, i.e. *H. fai* and *H. jenkinsii.* The trial runs were made by inclusion or exclusion of an entire species complex, e.g. exclude all members of the signifer complex, or exclude the two amphi-American *Himantura* and treating one of the species complex as the outgroup. Such treatment, while not expected to result in a significant change of the general topology due the relatively small data matrix, may help provide a clue to the relationship between the two closest taxa (Bremer *et al.* 1999). Thus, depending on which taxa or group of taxa was involved, a more structured relationship may be obtained. In this case, the relationship among the Indo-Pacific *Himantura* indicate *H. fai* as occupying the basal-most position when *H. granulata* was used as the outgroup (results not shown). In most cases however, bootstrap support for the relationships (among *Himantura*) never exceeded 50%.

Two observed varieties or forms of *H. gerrardi*, i.e. 'small denticle' and 'large denticle' (Figure 5.2.8), were included in the analysis as these two varieties were determined sufficient enough to be distinguished from each other. However, as seen from the resulting data matrix (Appendix 3.2.2), due to the selection of characters, both forms of *H. gerrardi* differ from each other in the data matrix by just one character (character 44, disc dorsal patterning either absent or present, or both absent and present), not including four other characters which are of unknown state in the latter.

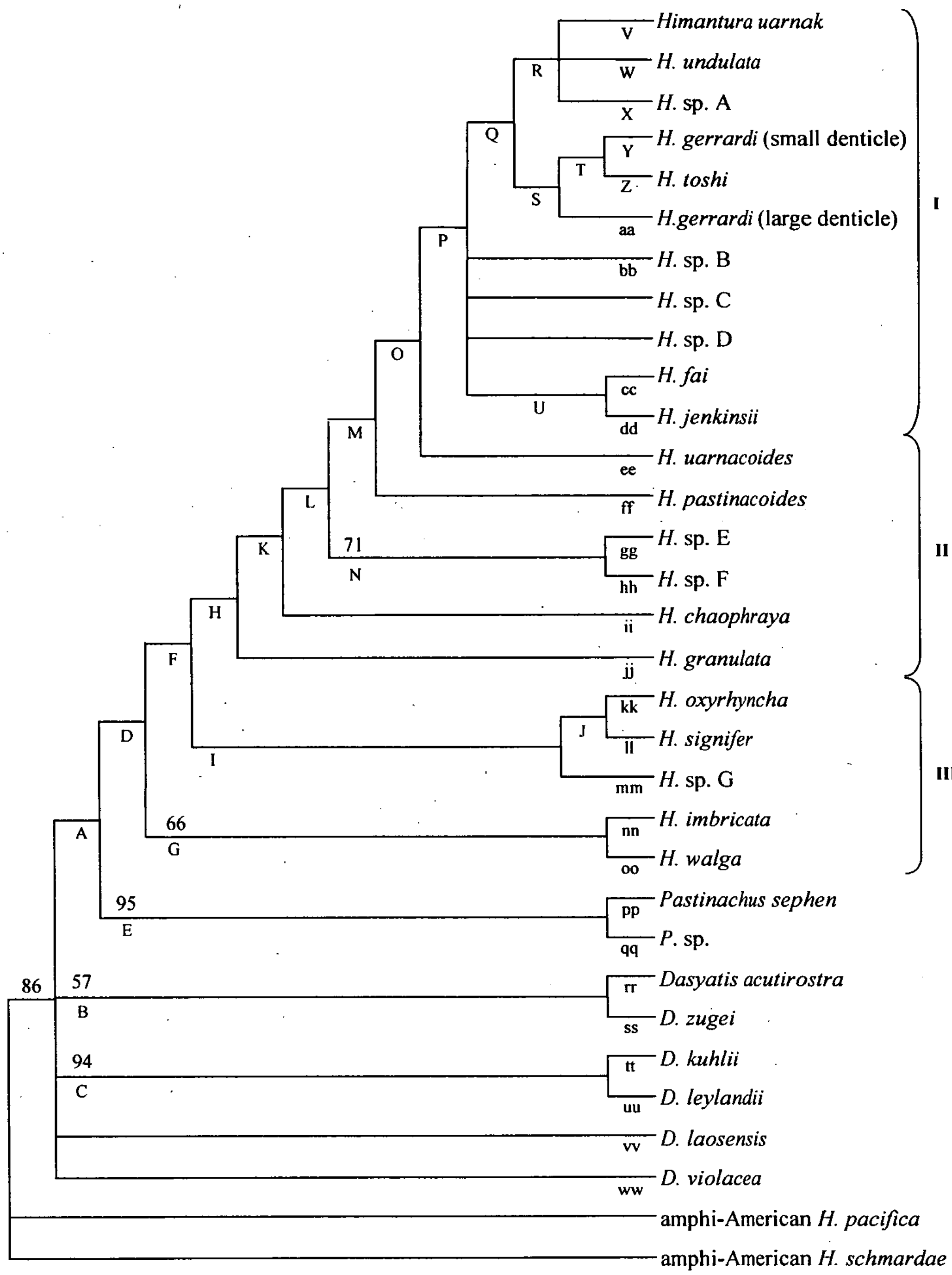

Figure 3.2.13. Strict consensus tree (tree length=166 steps, CI=0.39, RI=0.64, RC=0.25) for 32 taxa (including two forms of *H. gerrardi* and two outgroups amphi-American *H. pacifica* and *H. schmardae*). Numbers above branches indicate bootstrap support of ≥50% from 2000 replicates using fast step-wise addition. Letters below branches represent the following character changes, with states in parentheses and nonhomoplastic characters in bold (question mark before character number indicates character change if taxa with missing or unknown character state are excluded): A=20(1); B=**6(0)**, 10(0), 11(0); C=**?13(1)**, **?14(1)**, 26(1), 29(2), 36(0), 38(0), 41(1), 44(1), 45(0); D=**?14(2)**, **?15(1)**, 19(1), 27(1), 38(1); E=19(0), ?27(0), 38(0); F=21(1), 22(1), ?24(1), ?25(1), ?26(0), 35(0), 47(0); G=21(0), 22(&), ?24(0), ?25(0), ?26(2), 35(&), 47(&); H=46(1); I=46(0), 47(0); J=10(1), ?25(1), ?26(0), ?27(1), ?37(0), 39(0); K=17(1), 28(1), ?42(1); L=1(0); M=11(1), 29(1), 34(1); N=2(2), 11(0), 29(0), 34(0), 47(1); O=35(0); P=16(1); Q=44(1,&); R=?21(1), 25(1); S=?21(0), 25(0); T=?32(1), ?37(1), 44(&); U=31(0); V=2($); W=23(&), 26(1); X=41(0); Y=2(1); Z=2(&), ?21(0), ?41(1), 47($); aa=44(1); bb=45(&); cc=25(2), 30(1), 37(1), 39(0); dd=23(1); ee=16(0); ff=35(&); gg=25(2), 33(1), 35(0), 36(1), 39(0), 40(1); hh=25(1), 33(0), 35(1), 36(0), 39(1), 40(0); ii=1(1), 26(0), 36(&), 47(&); jj=11(&), 17(0), 22(&), 28(0), 42(0); kk=5(1), 16(1), 17(1), 28(1), 33(0), 44(1); ll=5(0), 16(0), 17(0), 28(0), 33(1), 44(0); mm=10(0), 39(1); nn=10(&), 33(0), 34(1); oo=10(1), 33(1), 34(0); pp=47($); qq=47(1); rr=4(0), 5(1), 7(0), 17(1), 19(1), 24(1), 47(2); ss=4(1), 5(0), 7(1), 17(0), 19(0), 24(0), 47(1); tt=3(0), 27(1), 35(&), 43(0); uu=3(1), 27(0), 35(0), 43(1); vv=9(0), 47(0); ww=1(1), 46(1). I='uarnak' complex; II='uarnacoides' complex; III='signifer' complex. See text for definition of complexes.

Various colour morphs found in other species, particularly *H.* sp. A (Appendix 3.1.1), were however, not included in the analysis. This was because the relationship between this species and its closest relative, *H. uarnak* and *H. undulata*, was already evident (node R; 21:1, presence of tertiary denticle band, and 25:1, infra-orbital loop extending to between the first and fifth gill slits) during the trial analyses. Moreover, information for the other forms of *H.* sp. A are largely lacking due to scarcity of study materials.

Two characters (character 40, presence or absence of anterolateral processes, and character 47, habitat distribution) which are rather weak, owing to the subjectivity of character coding for the former, and coding based entirely upon published reports of species distribution for the latter, was also included in the final analysis, as these two characters supported the relationship between species within the uarnacoides complex (Figure 3.2.13).

During initial character analysis of a data matrix which included the ingroup, and both distant (i.e. *R. typus* and *P. daviesi*) (McEachran *et al.* 1996) and closer outgroups (i.e. *H. pacifica* and *H. schmardae*) (Lovejoy 1996), it became clear that the two distant relatives retained many plesiomorphic characters. This contributes to the high number of autapomorphic character states, resulting in fewer variable (informative) characters. Furthermore, when both distant and closer outgroups were simultaneously used, the resulting tree could not be rooted without the ingroup maintained as monophyletic. Therefore, the outgroups were successively analysed separately, and the character matrix modified accordingly, when different outgroups were involved. For the final analysis, the distant outgroup was excluded from the data matrix.

3.3 DISCUSSION

The present study included almost all extant Indo-Pacific *Himantura*, except for one species which is treated as *incertae sedis* (Chapter 5). The species list, considered as the most updated, following a concurrent taxonomic revision of the genus (Chapters

2 and 5), was originally based on Compagno and Roberts (1982), and from unpublished works of P. Last (pers. comm.). Also included in the analyses were 7 new species (*H.* sp. A-G) discovered during the course of this study. The only two non Indo-Pacific *Himantura*, i.e. amphi-American *H. pacifica* and *H. schmardae* were treated as outgroups at the onset following Lovejoy (1996), McEachran *et al.* (1996), and Lovejoy *et al.* (1998).

The result of this analysis differs from previous studies (Nishida 1990; McEachran *et al.* 1996; Rosenberger 2001a), particularly the relationship between *Dasyatis* and *Himantura* species. The disparity in resolution between this study and the previous studies, as well as among the previous studies is attributed to several factors, i.e. differences in taxa analyzed, in characters used, and in character coding, as highlighted by McEachran *et al.* (1996). Moreover, as had been stressed by Nixon and Carpenter (1993), it is only when sampling of related taxa is more complete, can there be a greater expectation of stability in future studies.

It is noted that the identities of nominal species used in the analyses of several earlier phylogenetic studies are also questionable. For example, Nishida (1990) listed *H. bleekeri* in his work, a name considered as senior synonym of *H. uarnacoides* in the present study (Chapter 5). Comparison of the illustrated parts with supposed conspecifics from Sabah (Malaysia), revealed further differences. Nevertheless, it is noted that the internal structures (i.e. neurocranium, scapulocoracoid and pelvic girdle) are frequently distorted, and that the outlines of these structures as observed from x-ray plates may be deceiving. Therefore, the observed differences, particularly in fontanelle and scapulocoracoid shape (height) are presently treated as a parallax problem, until these can be independently verified.

Another example of questionable species identity is a work involving the molecular phylogeny of Asian stingrays (Sezaki *et al.* 1999). The identities of two species, *H. gerrardi* and *H. imbricata* were confirmed doubtful, after I examined the supposed specimens used in this study (H. Ishihara pers. comm.).

A separate *Himantura, Dasyatis* and *Pastinachus* is evident based on results of the present study (Figure 3.2.13). The Indo-Pacific *Himantura* formed a terminal clade (node D), with the two *Pastinachus* species basal to it. The clade supporting Indo-Pacific *Himantura* + *Pastinachus* spp. (node A) formed a polytomy with the *Dasyatis* species, but the deeper phylogeny among *Dasyatis* species was not resolved.

Characters supporting all Indo-Pacific *Himantura* as separate from the other two genera (i.e. *Dasyatis* and *Pastinachus*) comprising Indo-Pacific taxa are new characters, not previously used in earlier studies (Nishida 1990; McEachran *et al.* 1996; Rosenberger 2001a). These characters involved squamation and clasper characteristics. Hence, for the first time, other (additional) characters are demonstrably supportive of the traditional and exclusive use of tail fold character (its presence or absence) for distinguishing genera of the Family Dasyatidae, and these three genera in particular.

For the squamation characteristics, it is the presence of a secondary denticle band in adults and sub-adults of all Indo-Pacific *Himantura*, two *Pastinachus* species, and two amphi-American *Himantura* supporting each clade. However, it is noted that denticle shape and size among these three groups is unique. In the Indo-Pacific *Himantura*, denticles of the secondary band range from irregularly-shaped to rounded, with a smooth and flat crown. In *Pastinachus*, these are always angular (irregular) in shape, and arranged very close to each other, like a mosaic pattern. As for the amphi-American *Himantura*, the denticles are quadriradiate. The enlarged mid-scapular denticles in the amphi-American *Himantura* are also unique in that these occur as a paired structure, rather than singular or as a series, as is the case for members of the Indo-Pacific *Himantura* and *Pastinachus*.

Clasper characteristics (including clasper musculature and mixopterygial characteristics) of adult males of several dasyatid species have been phylogenetically examined and described by Nishida (1990). However, Nishida did not consider any of these in his phylogenetic analyses, primarily because specimens were unavailable for many of the taxa examined. On the other hand, Taniuchi and

Ishihara (1990) in comparing the clasper structures between freshwater representatives of Dasyatidae and Potamotrygonidae, suggested the clasper characteristics of these taxa were not phylogenetically informative.

In the present study, the phylogenetic importance of clasper characteristics in supporting the Indo-Pacific *Himantura* clade is shown. In particular are the presence or absence of a pseudosiphon and its position (if present) (character 14), and the presence or absence of a pseudorhipidion ('small flap' in Nishida) (character 15). Additionally, one mixopterygial character, i.e. shape of the terminal tip of axial cartilage (character 41), was considered in the analysis. This character was found to be homoplastic, the states found in both Indo-Pacific *Himantura* and *Dasyatis* species. Another clasper characteristic not considered in this study but seemingly important for inferring further the interrelationship among the *Dasyatis* species, is the margin of the hypopyle, whether smooth or somewhat pleated. A somewhat pleated or serrated hypopyle margin was observed only in two amphi-American *Dasyatis* (Figure 3.2.5w,x), and not in any of the Indo-Pacific *Dasyatis* taxa.

Ingroup relationships

The Indo-Pacific *Himantura* was found to form a separate clade from the Indo-Pacific *Dasyatis*, thus disputing the findings of previous studies (Lovejoy 1996; Rosenberger 2001a). The present analysis also suggests a pattern of species subgrouping within the Indo-Pacific *Himantura*, and the presence of sister relationships within each subgroup. These subgroups are provisionally defined herein as the '*uarnak*', '*uarnacoides*', and '*signifer*' complexes, as inferred from the strict consensus tree shown in Figure 3.2.13.

The three species complexes, of which only one is monophyletic (i.e. '*uarnak*' complex), the other two being paraphyletic, was primarily based on first-hand knowledge of the species involved. Thus, such a division might appear entirely arbitrary, as there is either only weak bootstrap support (less than 50% support) (Figure 3.2.13, values less than 50% not indicated), or no clear support for such clades (i.e. '*uarnacoides*' and '*signifer*' complex).

The absence of support is likely to reflect the disproportionate ratio of number of characters : number of taxa involved in the analysis, as demonstrated in other recent findings (e.g. McCracken & Sheldon 1998; Bremer *et al.* 1999; De Queiroz *et al.* 2002). According to Bremer *et al.*, a support value of 95% for a node would require the minimum number of characters to be three times as many as the number of nodes, with no homoplasy, with an even distribution of characters on the tree, and binary characters.

Species complexes

The '*uarnak*' complex is the largest of the three, comprising ten species including four new species (*H.* sp. A-D) ('I' in Figure 3.2.13). Members are supported by a single homoplastic synapomorphy (node P); cross section of tail circular (16:1). Nevertheless, other similarities among members are observed, i.e. they generally have patterned disc shape and/or banded tail. Three sister pairs are observed, although their deeper relationship, particularly with the new species (*H.* sp. B-D), is not resolved. This is attributed to missing data (Appendix 3.2.2), due to lack of materials.

The first sister clade, comprising *H. uarnak, H. undulata* and *H.* sp. A, is supported by two synapomorphies (node R). All three species have a patterned dorsal surface, on which spots are present at birth and transforming into varying degrees of reticulations with age. Thus, their identification based on disc colour patterns alone, as is the common practice, usually leads to misidentification, and most likely identified as *H. uarnak* (e.g. Sainsbury *et al.* 1985). In the present study, the use of squamation characteristics proved useful for distinguishing these patterned taxa more readily (Chapter 5).

The second sister pair of *H. gerrardi* (small denticle) + *H. toshi* is supported by three synapomorphies (node T). However, further analyses indicate only one of the three, i.e. disc dorsal patterning both absent and present (44:&), as unambiguously supporting this clade. The status of character change for the two other characters (character 32, supra-orbital crest either reduced to a keel along the dorsolateral margin of the orbital region, or plate-like; and character 37, scapulocoracoid height in lateral face, either equal to or shorter than wide, or taller than wide) is presently uncertain as these are unknown (treated as missing data) in the large denticle form of *H. gerrardi*, a sister to this sister pair (node S). Similar to the first sister pair, the second pair have a marked or patterned dorsal surface. However, it differs from the first by having the spotted dorsal surface retained throughout its lifetime. Moreover, *H. gerrardi* (small denticle) specimens examined were observed as having both a plain and spotted disc. This character also turned out to be the only synapomorphy (node Q) supporting a sister relationship between the *H. gerrardi* (large denticle) and *H. gerrardi* (small denticle) + *H. toshi* clade, and *H. uarnak* + *H. undulata* + *H.* sp. A.

The third sister pair comprising *H. fai* + *H. jenkinsii* is supported by a single synapomorphy (node U; mid-region of dorsal fontanelle greatly constricted; 31:0). However, during the trial analyses (Section 3.2.2), such a close relationship was not observed within the uarnak complex. Instead, *H. fai* occupied the basal-most position, and is plesiomorphic to *H. jenkinsii* (data not shown). Based on squamation characteristics, *H. fai* and *H. jenkinsii* are hypothesized as representing a transitional form between the more plesiomorphic and the more apomorphic taxa. In *H. fai*, denticle development is rather slow, and does not appear until the individual reaches a relatively large size (> 300 mm disc width); even at 630 mm disc width (CSIRO H2754.01), denticles are still sparse on the dorsal surface. Sparse denticle development is typical among the Indo-Pacific *Dasyatis* (plesiomorphic form), while 'heavier' denticle development is more typical among the Indo-Pacific *Himantura* (apomorphic form). For example, specimens of *D. acutirostra* are entirely naked at 296 mm and 351 mm disc width, whereas a denticle band is already developed by the same size in the *Himantura* (apart from *H. fai*), and denticles may have even developed pre-birth (e.g. in *H. uarnacoides*).

On the other hand, it is the presence of an enlarged row of denticles along the trunk to midline of the tail in *H. jenkinsii*, which is considered unique within this complex, but typical among members of the signifer complex. This character is polymorphic in *H. undulata*, as only one out of four specimens examined, displayed this character.

The '*uarnacoides*' complex ('II' in Figure 3.2.13) is comprised of 6 species, including 2 new species appearing as a sister pair (*H.* sp. E and *H.* sp. F). This complex is intermediate between the other two complexes, and is supported by a single synapomorphy (absence of sexual dental dimorphism; 46:1). Members have rounded disc apices (rather than angular), are generally uniformly coloured (adults of *H. granulata* usually with white specks, and prominent white tail), and grow to a very large size. The only sister pair (*H.* sp. E + *H.* sp. F) of this complex is supported by five synapomorphies (node N). The two new species have a striking resemblance to each other, in terms of general external morphology. However, there are also several striking differences between them, especially the extremely protrusible mouth, presence of angular cartilages, and prominent lateral prepelvic processes (in *H.* sp. F).

The basal-most complex, designated as '*signifer*' complex ('III' in Figure 3.2.13), comprises 5 species, including 1 new species (*H.* sp. G). Among the five, two pairs of sister species are evident, i.e. *H. imbricata* + *H. walga* (node G), and *H. oxyrhyncha* + *H. signifer* (node J). The latter pair forms a clade with *H.* sp. G (node I). Although there are no synapomorphies supporting a closer relationship between the *H. imbricata* + *H. walga*, and *H. oxyrhyncha* + *H. signifer* and *H.* sp. G clades, available (morphological and molecular) data suggest they are closer to each other (e.g. Compagno & Roberts 1982; Sezaki *et al.* 1999; Chapter 4) than to those of the other complexes, and in particular, regarding the maximum disc width. Members of the complex have relatively small maximum disc widths, and may not grow to a size bigger than 500 mm disc width. However, there is a record from Daro, Sarawak, of what appears to resemble a large *H. oxyrhyncha*. The record, based on an undated print colour photo (photo not scaled) was sent to Dr. Peter Last (pers. comm.) from a correspondent attached to that area. Additional data are required to verify the record.

The *H. imbricata* + *H. walga* clade is supported by 4 characters (node G). Both species appear very much alike in their general external morphology, and it is acknowledged that confusion currently exists regarding their identities (Chapter 5). In the present study, separation of these two species was primarily based on differences observed in their neurocranial structures (characters 33 and 34). Otherwise, the structure of their tails (tail more rounded and/or only weakly keeled in *H. walga*) appear as an important character for distinguishing species, although variations (in degree of tail keels) were detected in *H. imbricata*. Moreover, it appears mature females of *H. walga* usually display a thickened tail tip, becoming club-like.

The sister pair of *H. oxyrhyncha* + *H. signifer* (node J), and the *H. oxyrhyncha* + *H. signifer* and *H.* sp. G clade (node I) are each supported by two synapomorphies. Compared with the first sister pair (i.e. *H. imbricata* + *H. walga*), these three species are more readily distinguishable from each other by their dorsal disc colouration. The dorsal surface of the disc and tail are reticulated in *H. oxyrhyncha*, whereas uniform in *H. signifer* and *H.* sp. G (i.e. disc greyish, with a prominent white disc margin in *H. signifer*; disc entirely dark brown in *H.* sp. G), although some adults have been observed to possess several dark spots. Members of this clade are further distinguished from the *H. imbricata* + *H. walga* clade by their longer, whiplike tail. Examination of more materials, especially specimens of *H. imbricata*, might help reveal additional synapomorphies, namely patterns of the ventral lateral line canals.

Evolutionary trend of characters

Characters supporting the clades show a high degree of homoplasticity, although however, a pattern of character evolution may be derived from the resulting topology. These findings corroborate the results of previous studies, from which hypotheses regarding character evolution of the disc, tail and lateral line canal patterns have been proposed (Lovejoy 1996; McEachran *et al.* 1996; Rosenberger 2001a). Rosenberger in her study investigating the relationships within *Dasyatis*, discovered the disc and tail characters as being particularly homoplastic.

The general pattern of the disc shape and its attributes (Chapter 2) as observed from higher batoid phylogeny (Nishida 1990; Lovejoy 1996; McEachran *et al.* 1996; Compagno 1999a,b) indicate a transformation from one with a relatively shorter and less angular snout, with its pectoral-fin apices more obtusely angular and posterior disc margins more or less straight, to one with a relatively longer and more angular snout, with its pectoral-fin apices more acutely angular and posterior disc margins becoming convex.

The transformation of pectoral-fin apices becoming more acutely angular is also observed in the ontogenetic development of the disc shape, albeit very gradual, thus supporting (the strict interpretation) of Haeckel's Biogenetic Law (see Kitching *et al.* 1998). Within the ingroup, ontogenetic transformation of the disc shape is more readily observed when the smallest and largest individual of the same species are compared side by side (e.g. *H. toshi*, Figure 5.2.12; *H.* sp. A, Figure 5.2.23). Furthermore, as observed by Rosenberger (2001a), shorter snout length and convex anterior margin of the disc are indicative of a plesiomorphic form.

Both external and internal morphologies of tail characters are demonstrated as phylogenetically important in the present study. However, the importance of these characters, particularly absence or presence of tail skin fold, are de-emphasized. Treatment of the characters 'tail with weak keel' (in *H. walga*), and 'non-cartilaginous tail skin fold rudimentary' (in *H. imbricata* and *D. acutirostra*), as being the same character state (18:1; 19:1) in this study, although different from previous studies (Nishida 1990; Rosenberger 2001a), did not affect the present grouping of a separate Indo-Pacific *Himantura* and *Dasyatis* (e.g. Compagno 1999b). Instead, a more structured relationship among members of each genus is revealed for the first time.

The hypothesized absence of tail folds as the derived character state (Nishida 1990) is also supported in the present tree topology. The position of *D. acutirostra* (tail folds absent) as more basal to *Pastinachus* spp. (tail folds present) however, is indicative that absence of the tail folds may have evolved at least twice in the whip-tailed stingrays. Moreover, cartilaginous radials are absent in the tail folds (43:1) of the two *Pastinachus* species although the tail folds in these two are more conspicuous compared with that observed in all the other *Dasyatis* spp.

The evolutionary trend of other tail characters suggests circular tail base (16:1), and sting base not constricted (17:1), as derived from depressed tail base (16:0), and constricted sting base (17:0). The former characters are found in all members of the uarnak complex, the latter in all members of the signifer complex, two *Pastinachus*, in most *Dasyatis*, and in both the amphi-American *Himantura*. Both character states of these two characters are found among the Indo-Pacific *Dasyatis*.

Patterns of the ventral lateral line canals provided a rich pool of phylogenetic characters as suggested by Lovejoy (1996), McEachran *et al.* (1996) and Rosenberger (2001a). The evolutionary trend of the characters considered are in general agreement with findings of these earlier studies, in that extensive reticulation and looping of the infra-orbital loop (24:1), and infra-orbital loop extending beyond the first gill slit (25:1; 25:2) are indicative of apomorphic character states. However, there exists a disparity in character state coding for 'lateral hook formed by subpleural component of hyomandibular canal' (character 26, or Rosenberger's character 8) in *D. violacea*, between this and Rosenberger's work. Rosenberger coded the character as 'shallow' for this species, whereas in the present study, it is coded as 'absent' (26:0) following coding for *H. pacifica* by Lovejoy (1996: Figure 2A).

Apomorphic character state for several other morphological and physiological characters as based on the resulting topology, are indicated in the following: diplospondylous vertebrae, not extended to sting base (42:1); disc dorsal patterning, present (44:1); tail banding, present (45:0); sexual dental dimorphism, absent (46:1); and habitat distribution, marine (47:2).

Diplospondylous vertebrae not extended to sting base (42:1) is observed in all members of the uarnak complex, and in all except two members (*H. granulata* and *H.* sp. F) of the uarnacoides complex. The character is unknown (treated as missing) in the only two *H.* sp. F specimens available, as the tails of these two have been cut before the sting. However, this character is likely to be State 1 for this species. Diplospondylous vertebrae extended to or slightly beyond sting base (up to 10 centra) (42:0) is observed in the two outgroups and in all the *Dasyatis* species. In ancestral batoids (e.g. *R. typus* and *P. daviesi*), the vertebrae is extended to the caudal tip.

Disc dorsal colouration including banding of the tail is observed in most terminal taxa, but is also present in one basal ingroup taxon (*H. oxyrhyncha*), and in *D. kuhlii* and *D. leylandii*. As with disc shape, disc colouration and tail banding both display an ontogenetic development. Most often, the disc patterning follows a transformation from spottiness to reticulations, with the tail bands also transforming into reticulation, although at a slower rate (*H. uarnak*, *H. undulata*, and *H.* sp. A). In other species (*H. gerrardi*, *H.* sp. B-D) however, the spots (when present) remain so throughout its lifetime, although more subtle transformation of the degree of spotting may take place in adults (e.g. becoming crescentic in *H. gerrardi*).

Sexual dental dimorphism (mature males exhibiting acute and elongate tooth cusp) is observed in all members of the basal signifer complex (this character is presumed to be true for *H.* sp. G although only one mature male specimen was available for this species), and in all but one *Dasyatis* species. In *D. violacea*, both males and females exhibit acute and elongate tooth cusp, which is one of the unique characteristic of this species.

The fresh- and brackish-water distribution among members of the more basal species complexes suggests that advanced forms of the Indo-Pacific *Himantura* are derived from freshwater ancestors. On the other hand, several members of the Indo-Pacific *Dasyatis* also exhibit fresh- and brackish-water distribution, although the deeper relationship among these species was not resolved in the present study. It is noted that a similar pattern of closer relationship between freshwater and marine *Himantura*, and between freshwater and marine *Dasyatis* than between marine *Himantura* and marine *Dasyatis*, or between freshwater *Himantura* and freshwater *Dasyatis*, is reflected by molecular data (Sezaki *et al.* 1999). Such relationships suggest that the dasyatid stingrays may have indeed colonized fresh water several times, as hypothesized by Compagno and Cook (1995), and that the ancestors were of marine form.

As noted by Compagno and Roberts (1982), Southeast Asia is within an area once occupied by the Central or North Sundaland drainage basin. Based on the scattered freshwater populations of a new species, *H. signifer*, they described, they further suggest that several present major river systems (the Kapuas, Indragiri, Perak, and Chao Phraya) as perhaps all tributaries of this great river system during Pleistocene sea level minima (~2 million years ago).

3.4 CONCLUSION

This is the first species-level whipray phylogeny utilizing all extant species of the Indo-Pacific *Himantura*. The results indicate that Indo-Pacific *Himantura* is not monophyletic with *Dasyatis*, or even a subset of the genus as suggested by earlier studies (Lovejoy 1996; Rosenberger 2001a). Instead, it is shown to be a monophyletic group, comprising of at least three species complexes, as based on morphological, biological and physiological evidence.

On the other hand, the Indo-Pacific *Dasyatis* is shown to be polyphyletic, and as with the *Himantura*, there may even be a separate Indo-Pacific and Neotropical group. A third genus, *Pastinachus*, is basal to the Indo-Pacific *Himantura*, but forms a polytomy with members of the Indo-Pacific *Dasyatis*. However, as described earlier, there is sufficient evidence indicating a separate form of Indo-Pacific *Himantura*, *Pastinachus*, and Indo-Pacific *Dasyatis*.

Characters are highly homoplastic among the ingroup taxa, although specialized characteristics are also common. Only five of the 47 characters considered for phylogenetic analysis herein indicate non-homoplasticity, with one confirmed as non-homoplastic, while the other four are pending confirmation, until more data become available. The characters considered herein although extensive are not exhaustive; two characteristics not considered but may prove to be phylogenetically important are basibranchial cartilage (i.e. branchial arches and branchial skeleton), and musculature. Additional materials are required to improve the resolution of the present phylogeny, as several of the characters of taxa examined were unknown, due to lack of specimens.

CHAPTER 4

4.0 MOLECULAR PHYLOGENY

The Family Dasyatidae comprises batoid fishes commonly known as whip-tailed stingrays, whiprays, or stingrays. It is one of the major lineages of cartilaginous fishes inhabiting the marine and freshwater ecosystems of the tropical and sub-tropical regions. Most species have a widespread distribution, occurring throughout the marine ecosystem of the Indo-Pacific region, although other species particularly those found in freshwater habitats have a more limited distribution, or are endemic (e.g. Compagno & Cook 1995).

Compagno (1999a) tentatively recognized 23 species of *Himantura*, excluding four undescribed species, based on the synapomorphy of absence of a skin fold on the tail. Two of the species, *H. pacifica* and *H. schmardae* which are found only in the Neotropical region, were each preceded with a question mark, indicating tentative placement prior to formal taxonomic application for reassignment to another genus. Another species, *H. fluviatilis*, also indicated with a question mark, rather reflects the uncertainty relating to the nomenclature of this species. These examples demonstrate only a fraction of the problems existing in stingray taxonomy and systematics (e.g. Last 1979; Compagno & Roberts 1982; Last & Stevens 1994).

That the genus *Himantura* is not monophyletic, was first expressly stated by Compagno and Roberts (1982) in their taxonomic revision of the genus. They hypothesized the presence of one or more inclusive groups within the genus, which included species from both the Indo-West Pacific and Neotropical regions, based on the disc shape and the number of functional stings (i.e. either oval-shaped with usually two stings, or diamond-shaped or angular disc with usually one sting). Last (in Whittington & Last 1994; pers. comm.) later confirmed that the genus is polyphyletic based on his unpublished data on the revision of the family, and agreed with the conservative synonymy scheme proposed by Compagno and Roberts. Last (pers. comm.) hypothesized species complexes among the genus based on disc shape, colour pattern and squamation.

A notable fact observed among species of *Himantura* is the huge difference in size. For example the maximum size of *H. imbricata* which is approximately 300 mm disc width (Compagno & Heemstra 1984), is also the birth size for a *H. chaophraya* litter (Monkolprasit & Roberts 1990). At maturity, the latter species reaches to about 1 m in disc width, and may develop further to attain a body weight of 500 - 600 kg (Monkolprasit & Roberts).

The need to reassign the two Neotropical or amphi-American *Himantura* species may be traced back to the work carried out by Lovejoy (1996). In his study, Lovejoy investigated the phylogeny of the Neotropical freshwater stingray family Potamotrygonidae, using morpho-anatomical and physiological approaches. His results confirmed a polyphyletic *Himantura*, which prompted him to suggest a separation between the amphi-American and the Indo-West Pacific species. The former group (comprising the two species mentioned earlier), was determined to be a sister group to the potamotrygonids, whilst the latter formed a trichotomy with other members of the dasyatid family, particularly *Dasyatis* spp., and the more advanced ray taxa comprising gymnurids and myliobatoids. The sister relationship between the two amphi-American *Himantura*'s and the potamotrygonids was later corroborated with molecular evidence based on a study using partial DNA sequence of the cytochrome *b* gene (Lovejoy *et al.* 1998).

At about the same time as Lovejoy's (1996) work, McEachran *et al.* (1996) carried out a similar study to investigate the phylogeny of all the batoids (which included the shark-like form as well as the more typical discoid form). The result of their study corroborated Lovejoy's findings regarding a paraphyletic Dasyatidae. More recently, Rosenberger (2001a) in assessing the phylogenetic relationship among species of the genus *Dasyatis*, further confirmed this genus as not monophyletic.

It is noted that as with the genus *Himantura*, the genus *Dasyatis* comprise amphi-American and Indo-Pacific species. The *Dasyatis* species included in Lovejoy's (1996) study were apparently all amphi-American *Dasyatis* species, except for two species, which is *D. violacea*, a cirgumglobal pelagic species (although there is no confirmed report to date on the occurrence this species in the Indo-West Pacific), and *D. purpureus*, an ambiguous species described from Durban Bay, South Africa (Wallace 1967; see Compagno & Heemstra 1984; Chapter 5). On the other hand, only one Indo-Pacific *Himantura*, *H. fai*, was included in the study (Lovejoy). McEachran *et al.* (1996) also appeared to have included only amphi-American *Dasyatis* species, including *D. violacea* in their study (one unidentified species is presumably also from the Neotropical region), and according to them, lumped the Indo-West Pacific *Himantura* species with *Dasyatis* following Lovejoy. However, no Indo-West Pacific *Himantura* species were given in their list of specimens examined. Rosenberger's (2001a) assessment included one species of Indo-West Pacific *Himantura*, *H. gerrardi*, and *Dasyatis* species from both regions, being *D. kuhlii* and *D. zugei* from the Indo-West Pacific and the rest from the Neotropical region.

In another study investigating the phylogeny of the myliobatoid whiprays (i.e. all discoid rays) (Nishida 1990), the non monophyletic relationship of the family Dasyatidae was not detected. In fact, the endemic freshwater stingrays of South America were lumped under the same family (Dasyatidae) as the Indo-Pacific taxa (Nishida). Apparently, in his analysis Nishida included both Neotropical and Indo-Pacific *Dasyatis* species, three Indo-Pacific *Himantura* species, but no Neotropical *Himantura* species.

The current generic classification of marine and freshwater Indo-Pacific whipray taxa, particularly the genera *Himantura, Dasyatis* and *Pastinachus* (e.g. Compagno 1999a, b), based on the synapomorphy of absence or presence of tail skin fold, is supported, by morphological (Chapter 3) and molecular studies (Sezaki *et al.* 1999). However, except in *Pastinachus*, the relationships among species assigned within these genera are poly- and para- phyletic. The deeper phylogenetic relationship among the three genera remains unclear, due to low bootstrap support for the clades; this was despite including all extant Indo-Pacific *Himantura* (Chapter 3), and sequencing the entire cytochrome *b* gene (Sezaki *et al.*).

Chen (*in press*) also reported the paraphyly of dasyatid genera, particularly *Dasyatis, Himantura, Taeniura* and *Urogymnus*, based on analysis of the complete mitochondrial 12S rRNA gene. However, details regarding the species included in his study were not available at the time of writing, as only an abstract of the study (presented at the 80^{th} Annual Meeting of the American Society of Ichthyologists and Herpetologists, June 14-20, 2000) was available. It is possible however, that Chen's study may have included species from both regions (i.e. Neotropical and Indo-West Pacific), and if so, his results may further corroborate the findings by Lovejoy (1996), McEachran *et al.* (1996) and Rosenberger (2001a) on the presence of Neotropical and Indo-West Pacific species.

Molecular techniques are particularly useful for analysing relationships among morphologically conserved taxa, such as elasmobranch fishes, as they offer new suites of characters which otherwise are quite limited. Furthermore, it has been shown in other studies that sequence characters have revealed some cryptic species and helped to identify some incorrectly split groups (reviewed by Stepien & Kocher 1997). However, the interpretation of results from molecular phylogenetic studies is useful only when a comparison for taxonomic congruence can be made with morphologically based phylogeny (e.g. Penny *et al.* 1990). With molecular (sequence) data, the main problems associated with discerning a relationship lies in the identification of homologous characters, and in finding sufficient number of synapomorphies of shared common ancestry rather than as a result of homoplastic convergence (Stepien & Kocher).

It is the aim of this study to utilize molecular techniques for discerning cryptic stingray species among the genus *Himantura*. Cryptic species exhibiting an array of colour pattern in the same, or different life-stages, e.g. *H. uarnak* and *H. gerrardi* are an example of some of the challenges faced by taxonomists, and in more practical situations, by fisheries personnel involved in species identification for fisheries data collection. The focus of this study are the Indo-Pacific *Himantura* species, as it has been shown that these are sufficiently separate from their (two) amphi-American congeners, as discussed above. This study attempts to taxonomically review the genus by constructing molecular and morphological based phylogenies.

4.1 MATERIAL AND METHODS

The technique adopted in this study is based on nucleotide sequencing using the polymerase chain reaction (PCR), currently a standard tool in molecular systematics (Palumbi 1996; Stepien & Kocher 1997). Two universal animal mitochondrial (mt) genes, i.e. 16S - the large subunit ribosomal RNA gene in mtDNA, and cytochrome *b* - a protein encoding gene of the mitochondrial genome, were selected for DNA sequencing. The cytochrome *b* was selected primarily because of its wide application in fishes (review by Stepien & Kocher), whereas 16S a more conserved non-coding gene was selected to complement the first gene.

4.1.1 Tissue collection and preservation

Skeletal muscle tissue was used as the source of DNA for extraction. Sampling was done *in situ* from freshly killed or fresh frozen whole fish from fish markets, during a 1999 field trip to the Malaysian states of Sabah and Sarawak, and voucher specimens retained whenever possible (refer 'Materials' in Chapter 2). Fish sampled from these markets were usually in good condition and were also generally very fresh (pers. observation), which is important in ensuring a yield of good quality DNA (Dessauer *et al.* 1996). Muscle tissue was taken by making an incision through the skin using a scalpel blade, from either of two positions: on the dorso-lateral surface of the tail base, or from the thickest part (mid-disc on the pectoral-fin) on the ventral surface of the fish. Tissues were extracted from as 'deep' as possible, away from the surface. About 0.5 cm^3 of flesh was collected for each sample, which was placed directly into 1.5 ml microcentrifuge tubes containing absolute (90-99%) ethanol, for preservation, and stored at 4^0C until required. Duplicate tissue samples were taken for most samples, and for each sample (including duplicates), a new scalpel blade was used to avoid cross contamination between samples.

Tissue samples were also donated by colleagues, and were received as either: preserved (75-99% ethanol), frozen (stored in -80^0C) or extracted DNA in 25 μl buffer (Tris-EDTA). Appendix 4.1.1 gives details (species, specimen registration number, specimen locality, and collector) of the tissue samples used.

4.1.2 Laboratory procedures

All laboratory procedures were conducted under contained environmental conditions to avoid contamination from exogenous DNA, with a separate room for DNA extraction and PCR reactions. Additional precautions were also taken, such as routine cleaning of the bench area using concentrated sodium hypochlorite before commencing work, and the autoclaving of all plastic-ware (pipette tips, pestles and microcentrifuge tubes) and dH_2O at 121^0C for 20 min prior to use. Exposure of plastic-ware and dH_2O to short wave uv radiation (254 nm) for 10 min was occasionally done as an alternative to autoclaving. Laboratory procedures involved extraction of DNA from samples, DNA amplification and DNA sequencing.

4.1.2.1 DNA extraction

Total DNA extraction from the samples were carried out using either one of two extraction protocols, i.e. CTAB extraction, or QIAGEN's QIAamp® Tissue Kit. The second method, a less time-consuming but more costly alternative, was mainly employed on samples that failed to yield sufficient DNA using the first method. For both methods, only a fraction of tissue sample per extraction was used, approximately 100 mg and 25 mg respectively.

4.1.2.1a CTAB extraction

All ethanol preserved tissue was rinsed in distilled water. Frozen tissue was used directly without washing. Tissue was placed into a 1.5 ml microcentrifuge tube containing 200 μl of 2x CTAB extraction buffer (2% w/v CTAB (hexadecyltrimethylammonium bromide), 1.4 M sodium chloride, 0.1 M Tris-HCl pH 8.0, 0.02 M EDTA), then ground using a plastic pestle to form a homogenous slurry. Another 400 μl of CTAB buffer was added, and grinding continued until all the tissue had been homogenized. The homogenates were then digested by adding 5 μl of 20 mg/ml proteinase K, vortexed briefly, and then incubated at 65^0C for at least one hour. During incubation, the homogenates were vortexed every 20 min and reground using a new clean pestle. Following incubation, 600 μl of CI (chloroform: isoamylalcohol, 24:1) was added into each tube, and the tubes shaken vigorously for about 1 min, before centrifuging at 13 000 rpm for 20 min. The resulting supernatant was transferred to a new 1.5 ml microcentrifuge tube containing PCI (phenol: chloroform: isoamylalcohol, 25:24:1), and extracted by shaking for 1 min followed by centrifuging at 13 000 rpm for 10 min. Samples were re-extracted with PCI subject to the clarity of the upper aqueous layer, as determined by visual observation, and in this study, all samples were treated with PCI at least twice. As a final step, CI was added to remove any last traces of phenol. The upper aqueous layer was then transferred to a new 1.5 ml microcentrifuge tube containing 700 µl of cold iso-propanol. The tubes were then placed on ice for 10 min to allow DNA precipitation, before centrifuging at 13 000 rpm for 20 min. Following this, the supernatant was pipetted out and 500 µl of cold 70% ethanol added. The tube was inverted gently and centrifuged at 13 000 rpm for another 10 min. The ethanol was pipetted off, and the DNA pellet dried under vacuum. Pellets were resuspended in up to 50 µl of dH_2O and allowed to rehydrate at 4^0C for 3-12 hours. Finally, the DNA was stored at -20^0C for later use as a template in PCR-amplifications.

4.1.2.1b QIAamp® tissue kit

The commercially available QIAamp® tissue kit from QIAGEN guarantees to purify DNA of size up to 50 kb, with fragments of approximately 30 kb predominating. The purification procedure is comprised of three steps; sample lysis, lysate binding and DNA elution, carried out using QIAamp spin columns in a standard microfuge. The procedures were carried out according to the manufacturers' protocol for 25 mg of tissue per sample.

4.1.2.2 PCR-amplification and assessment

The PCR technique, developed for *in vitro* synthesis of DNA, was adopted to amplify DNA. The method involves a cycle of three consecutive steps, denaturation (of double-stranded DNA), annealing (of extension primers to sites flanking the region to be amplified), and extension (of primers), conducted in the presence of a DNA polymerase (Avise 1994; Palumbi 1996).

Two primer pairs, 16Sar-L (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr-H (5'-CCGGTCTGAACTCAGATCACGT-3'), and CB1-L (5'-CCATCCCAACATC TCAGCATGATGAAA-3') and CB2-H (5'-CCCTCAGAATGATATTTGTCCTC A-3') were used (Palumbi *et al.* 1991; Palumbi 1996), which amplified DNA fragments of about 600 bp and 300 bp, respectively.

PCR-amplification took place in a 50 μl volume containing the following reagents, 25-100 ng genomic DNA, 10X buffer (10 mM Tris-HCl pH 8.3, 1.5 mM $MgCl_2$, 50 mM KCl, 0.01% NP-40, and 0.01% Triton X 100), 1.5-2.5 mM $MgCl_2$, 0.2 mM of each deoxynucleotide triphosphate (dNTP) (Amresco), 0.2 μM of each primer, 50 μg Bovine serum albumin (BSA) (New England BioLabs), 1 unit of *Taq* polymerase (Fisher Biotech International Limited), and dH_2O. Thermal cycling was performed in an MJ Research PTC 200 DNA engine. In every PCR experiment, a positive (containing a template known to amplify well) and a negative (containing no template, i.e. dH_2O) control were used. The PCR reaction was discarded if there were signs of contamination. Three thermal cycling conditions were used, of which at least one worked for each sample. All three conditions employed a preliminary denaturation step of 94^0C for 240 sec, modified annealing temperature profile's, followed by a post-extension step of 72^0C for 300 sec, before rapid ramping to 4^0C. The first temperature profile included 30 sec at 94^0C, 60 sec at 55^0C, and 90 sec at 72^0C. In the second condition, the cycles were separated into two blocks as follows: 10 cycles of 30 sec at 94^0C, 45 sec at 49^0C, and 90 sec at 72^0C, followed by 25 cycles of 30 sec at 94^0C, 45 sec at 55^0C, and 90 sec at 72^0C. For the third condition, cycles were also separated into two blocks as follows: first 5 cycles, 30 sec at 94^0C, 30 sec at 50^0C, and 60 sec at 72^0C, followed by 30 cycles of 30 sec at 94^0C, 30 sec at 56^0C, and 60 sec at 72^0C. The optimal PCR conditions used for the sequences obtained in this study are given in Appendix 4.1.2.

Following amplification, the PCR products were electrophoresed through a 1% agarose gel containing 50 μg ethidium bromide (EtBr) in TBE buffer (0.089 M Tris, 0.089 M Boric acid, 0.002 M EDTA) at 88 V for approximately 30 min. For the purpose of assessing PCR product fragment size, a molecular weight standard (100 bp DNA ladder, Geneworks) was always run with the samples. The DNA fragments were visualized under ultra violet light, and photographed.

4.1.2.3 PCR purification and quantification

Two methods were used to purify DNA, i.e. gel extraction and column purification.

4.1.2.3a Qiaquick® gel extraction protocol (QIAGEN)

The PCR products were re-run on a gel using the same conditions as for DNA fragment visualization. The DNA band was excised from the gel under ultra violet (uv) illumination, while ensuring the bands were not excessively exposed to ultra violet light. Gel slices were placed into separate pre-weighed 1.5 ml microcentrifuge tubes. The weight of each excised gel was used to determine the amount of Buffer QG to add. The gel was completely dissolved by incubation at 50^0C for 10 min. To help increase the yield of DNA fragments (< 500 bp), 1 gel volume of isopropanol was added to the sample and mixed. To bind DNA, the samples were loaded on to a QIAquick spin column, and centrifuged for 1 min at 13 000 rpm. The flow-through was discarded, and the spin column placed back into the same collection tube. Buffer PE (0.75 ml) was then added to the spin column to wash the DNA, and the column centrifuged for 1 min. The flow-through was discarded and the column centrifuged for 1 min. The spin column was then placed into a clean 1.5 ml microcentrifuge tube for the final step of DNA elution. Warmed (to 65^0C) distilled/ milliQ water was added to the centre of the column, and the column centrifuged for 1 min. The amount of water used was either 30 or 50 µl, depending on the intensity of the band under uv light, noted following electrophoresis. Purified DNA samples were stored at -20^0C.

4.1.2.3b Concert^{TM} (Invitrogen) rapid PCR purification protocol

This method is similar to the first method, except that a gel extraction step was not involved, thus minimizing loss of DNA. To bind DNA, 400 µl of Binding Solution (H1) was added directly to the PCR product and mixed thoroughly. The mix was loaded into the Concert^{TM} spin column, and centrifuged for 1 min at 13 000 rpm. The flow-through was discarded, and the column placed back into the same collection tube. Next, wash buffer (H2) were added, and the column centrifuged for

1 min. The flow-through was discarded, and centrifuging was repeated for another 1 min to remove all residual wash buffer. For DNA elution, the spin column was placed into a 1.5 ml recovery tube. DNA was eluted by adding 30 µl of preheated (65^{0}C) distilled/ milliQ water. The columns were then incubated at room temperature for another minute, before centrifuging again for 2 min. Purified DNA was stored at -20^{0}C.

4.1.2.3c PCR quantification

Purified PCR product was quantified using a VersaFluor™ fluorometer (Bio-rad), and concentrations recorded as ng/µl. The fluorometer was calibrated using calf thymus DNA for low range assay (100 ng/µl). 2 ml of freshly-made assay solution containing 10 mM Tris, 1 mM EDTA, 0.2 M NaCl and 100 ng/ml H 33258 dye was used to determine the concentration from 2 µl of purified PCR product.

4.1.2.4 Nucleotide sequencing

DNA nucleotide sequencing was carried out using BigDye terminator sequencing reactions (ABI), and determined for one or both DNA strands. Using this method, DNA fragments were fluorescently-labeled, which allows for analysis using an automated DNA sequencer (Ferl *et al.* 1991). In this study, an ABI Prism 377 automated DNA sequencer (PE Applied Biosystems, USA) was used to separate the extension products, and the sequencing products analysed using Sequence Navigator version 3.3 (PE Applied Biosystems, USA).

The light strand (L) was predominantly sequenced, and the heavy strand (H) sequenced only to confirm poorly resolved nucleotide sequences in the light strand. The sequencing reaction volume was 10 µl, with constant volumes of dye terminator (4 µl), 3.2 pmol of primer, 20-40 ng DNA per sequencing reaction, and dH_2O to 10 µl. Extension products were purified following "Ethanol precipitation protocol 1" (ABI). Samples were pipetted into a 1.5 ml microcentrifuge tube containing 2 volumes of 95% ethanol and 1 µl 3M sodium acetate. The mixture was thoroughly mixed by vortexing, placed on ice for 10 min, and centrifuged at 13 000 rpm for 25 min. The alcohol solution was then aspirated, and 190 µl 70% ethanol added to rinse the pellet which had formed on the bottom of the tubes. The ethanol was aspirated and the pellets were dried in a vacuum centrifuge for 10 min or until thoroughly dried. Dried DNA pellets were stored at 4^0C until analysed.

4.1.3 Data analysis (Phylogenetic inference)

Several strategies for phylogenetic inference from nucleotide sequences exist (Hillis *et al.* 1996; Simmons & Ochoterena 2000), all of which have varying influence on the resulting phylogenetic estimations (review by Lutzoni *et al.* 2000). The strategy adopted in the data analysis was to treat both sequence alignment and phylogenetic analysis as part of the whole process of phylogenetic inference. Thus, in an effort to find the most plausible sequence alignment for a particular data set, and ensuring that orthologous sequences are compared (Swofford *et al.* 1996), the replicable method of minimum cost multiple sequence alignment (Gatesy *et al.* 1993), and the phylogenetic weighting of alignments as suggested by Mindell (1991) were incorporated into the sequence alignment strategy.

4.1.3.1 Sequence alignment

Sequence alignment was aided by the computer software Sequence Navigator v.3.3 (PE Applied Biosystems, USA), and CLUSTAL X (Thompson *et al.* 1997) on a conventional Macintosh interface. All sequence data were initially evaluated using Sequence Navigator prior to alignment. During this preliminary analysis, the state of the nucleotide sequences was determined. Poorly resolved sequence data were eliminated, while other sequences including those partly readable were retained. Sequences were aligned by eye using the best sequence(s) as a reference to edit poorer sequences. The DNA sequences were confirmed by performing similarity searches against GenBank (Ouellette 1998; Benson *et al.* 2000) using the BLAST algorithm (Altschul *et al.* 1990). Access to the database was made electronically via the National Center for Biotechnology Information (NCBI) web page (see ref.). Further analysis of the refined sequences was conducted using CLUSTAL X. This software was utilised to produce the final sequence alignment.

The method suggested by Gatesy *et al.* (1993) requires the input of several sets of gap penalties/cost (gap opening, GO) and nucleotide substitution cost (gap extension, GE) for multiple alignment. This was implemented in CLUSTAL X by inputting the gap values in the MULTIPLE ALIGNMENT PARAMETER menu under MULTIPLE ALIGNMENT MODE. Additionally, under the same mode, CLUSTAL X also allows for two other alignment parameters, i.e. Delay Divergent Sequence and Transition Weight. However, for all alignments, these two parameters were kept constant at the default value of 40% and 0.5, respectively. The gap penalty ratios trialled were: 0.67:1, 10:1, 15:1, 20:1, 20:3, 30:1, 40:1, and 50:1. All alignments were repeated using the raw data file. The entire alignment was then scrutinized in relation to independent phylogenetic evidence and assumptions that can be made concerning the base-substitution processes. The option to generate a guide tree was also used, whereby, based on extrinsic data, the topology of the competing trees was compared to help determine the most optimal resolution.

Inclusion of an outgroup taxon involved the realignment of the data set, and applying the same treatment for searching for an optimal gap penalty set with only the ingroup taxa included.

4.1.3.2 Phylogenetic analysis

As with the morphological phylogenetic analysis, the molecular phylogenetic analyses, including statistical tests undertaken herein were conducted using PAUP* 4.0b8 (Swofford 2000).

4.1.3.2a Phylogenetic signal

The aligned sequence data sets were separately assessed for phylogenetic information content or signal, using the 'skewness of tree length-frequency distributions' method (Hillis & Huelsenbeck 1992). Distributions of tree lengths with a strong left skew were shown to indicate that relatively few solutions exist near the optimal solution (i.e. shortest tree) compared to elsewhere in the distribution, which in turn indicates there is a correlation among characters beyond that expected at random. The skewness test statistic, g_1, generated from a particular data set is compared against a set of critical values (Hillis & Huelsenbeck) to determine the level of phylogenetic signal. These values were shown to be relatively constant when the number of taxa examined is 15 or more, although these may be improved with the increase in number of randomly sampled trees from the tree length distribution (Hillis & Huelsenbeck). In this study, the g_1 values from 1 000 000 random trees with a nine-digit random seed value were obtained from the EVALUATE RANDOM TREES option of PAUP*.

4.1.3.2b Partition homogeneity test

A partition homogeneity test was conducted to test for significance of congruity (Farris *et al.* 1995) between the two gene data matrices. The null hypothesis of congruence would be rejected if the measure of incongruence (*D*, or, *P*, as implemented in PAUP*) was less than the critical value of 5%. In other words, incongruity between the data sets is indicated when $P \leq 0.05$. This test was carried out to analyse 200 random partition replicates using a heuristic search strategy with the tree-bisection-reconnection (TBR) branch-swapping algorithm, and simple stepwise addition, holding 5 trees at each step.

4.1.3.2c Analytical approach

The sequence data sets were phylogenetically analysed using both parsimony and distance methods. Using parsimony methods, a tree is found by the least number of discrete steps for all the base differences in a multiple sequence alignment, i.e. the number of evolutionary steps required to explain a given set of data. In this study, the optimality criterion based on Fitch and Wagner Parsimony or maximum-parsimony, i.e. no or minimal constraints on permissible character-state changes, which is also the simplest form of parsimony methods (see Swofford *et al.* 1996) was adopted.

Distance methods, as with maximum-likelihood methods, attempt to account for unobserved as well as observed substitutions in the data, based on a model of evolutionary change. Specifically, distance analysis estimates a corrected distance, i.e. the true evolutionary distance between a pair of sequences (see Swofford *et al.* 1996). The conceptual perspective of the method is to fit a particular mathematical model, i.e. an additive tree (a phylogenetic tree in which the distance between any two points is the sum of the lengths of the branches along the path connecting two points), and find an optimal value for the parameters (the branching pattern and the branch lengths) (Swofford *et al.*).

In this study, the increasingly popular minimum evolution (ME) method of Rzhetsky and Nei (1992a, 1992b, 1993) was adopted (Swofford *et al.* 1996). The optimality criterion of this method is 'that the tree with the smallest sum of branch length estimates is most likely to be the true one' (Rzhetsky & Nei 1993). In other words, all possible topologies of an unrooted bifurcating tree are computed, and the minimum value of the sum of all the branches chosen.

All phylogenetic analyses using parsimony involved character weighting (see Section 4.1.3.3), while all distance analyses (ME) involved an equal or unweighted character substitution rate only.

4.1.3.2d Heuristic search strategy

The heuristic search strategy was employed for both optimality criteria because of the large data set (>10 taxa) involved (Swofford *et al.* 1996), i.e. 60 and 41 taxa including two outgroups for 16S and cytochrome *b*, respectively.

Starting points (trees) were obtained by TBR branch-swapping, and 100 replicates of random stepwise addition, holding 5 trees at each step for all searches. Initial branch swapping in each replicate was constrained by limiting the number of trees saved to 200 and their length not less than 100. The search was repeated using one value less than the best score (shortest length) generated from the initial search.

For ME analyses, the search option allowing negative branch-lengths, and set to zero for tree-score calculation, was used. Distance measures were performed using the HKY85, Hasegawa-Kishino-Yano model (Hasegawa *et al.* 1985). This model generalizes the more popularly applied K2P model (Kimura's 1980 two-parameter model) to allow unequal equilibrium (2 substitution types, i.e. transitions vs. transversions) of base frequencies. (The K2P model takes into account the common observation that transitions and transversions occur at different rates, but still assumes equal base frequencies).

4.1.3.2e Gap treatment

There is considerable debate in the literature on the most appropriate method of gap handling (e.g. Hershkovitz & Leipe 1998; Lutzoni *et al.* 2000; Simmons & Ochoterena 2000). In this study, three regions in which a particular gap is positioned within the aligned sequence data sets, were identified. These were terminal positions, alignment-ambiguous region(s) and alignment-invariant regions. The first region is applicable for both coding and non-coding genes, whereas the latter two regions are only applicable for the non-coding gene. Thus, the 'status' of a gap and its subsequent treatment in the analyses was determined by its position within the aligned data set.

Gaps occupying a terminal position were treated as missing, as these were present as the result of 'sequence noise' and of length variability. Gaps in alignment-ambiguous regions (as identified using the method suggested by Gatesy *et al.* (1993); refer 'Sequence alignment' in Section 4.1.3.1) on the other hand, were entirely excluded from the final sequence analysis. The reason being to ensure only orthologous sequences were compared (Moritz & Hillis 1996; Swofford *et al.* 1996). As for gaps in alignment-invariant regions, one of two methods for their subsequent treatment was used. In the first instance, the gap(s) in the regions remained unaltered with different gap penalties set, the assumption being the existence of such a character is probably real. Thus, such gaps were treated as a 'fifth base' where the option is available (i.e. in parsimony analyses). In the second instance, only one sequence representing the same species exhibited the presence of an 'extra' nucleotide. Characters such as the latter, i.e. not nested within the more variable regions of the sequence, were presumed to be attributed to 'mechanical error', especially if there was more than one representative of the same taxon that did not exhibit the extra nucleotide. Such gaps were excluded from the analysis.

4.1.3.2f Tree evaluation

Consensus trees were evaluated by means of nonparametric bootstrapping (Felsenstein 1985). Bootstrap searches were achieved using fast stepwise-addition, as it had been suggested that estimates using fast bootstrap methods are similar to the exhaustive methods (Mort *et al.* 2000). Therefore, the results are not likely to affect the phylogenetic interpretation of the data. Two thousand bootstrap replicates were run (Hedges 1992). Replicates of 10 000 and 100 000 fast stepwise-addition bootstraps produced congruent tree topologies with bootstrap values varying by no more than 1%.

4.1.3.3 Molecular analysis

4.1.3.3a Character analysis

Several character weighting options i.e. equal, differential (transversions versus transitions), and transversion only were initially performed for all parsimony analyses of the DNA sequences. Such a conservative approach was adopted primarily to demonstrate the assumption that the two kinds of base substitutions (transitions and transversions) have different rates (e.g. Hasegawa *et al.* 1985), and with an expectation that weighted analyses *should* yield (a) better tree(s).

Increasingly however, character analysis at each codon position (of protein-coding genes) and the implementation of weighting schemes based on codon position have been shown to be better justified. Differential weighting based on unique saturation levels at these sites, particularly the third position, have all improved the resolution of parsimony analysis (e.g. Hackett 1996; Lydeard & Roe 1997; Maekawa *et al.* 1999). In another study, phylogenetic signal was detected within transition substitutions (Broughton *et al.* 2000). Therefore, excluding transitions entirely from phylogenetic analysis may not be the best approach for obtaining resolution in a phylogenetic estimation.

4.1.3.3b Saturation analysis

Weights for transversions were determined by saturation analysis or assessment of multiple substitutions at single sites of both genes. Assignment of transversion weight was then realized via a cost-matrix.

Evaluation of the potential for saturation of sequence variation within each data set was made by plotting transitions versus transversions. Evaluation of the patterns of sequence evolution was made by plotting pair-wise transition and pair-wise transversion values against two different estimates of percent divergence that serve as approximations of time since divergence: the uncorrected pair-wise divergence 'p' (Nei 1987), and Hasegawa-Kishino-Yano genetic distances (Hasegawa *et al.* 1985).

Saturation of each substitution type including those at each codon position was graphically assessed by the patterns of changes to sequence divergence of the respective scatter plots, with the inclusion of a distant outgroup (Hackett 1996), i.e. saturation was judged to have taken place if the scatter of points shows a plateau with increasing sequence divergence.

Alternatively, saturation levels may be assessed by the slope of the linear regression. When no saturation is observed in the data set, the slope equals one; with increasing saturation level, the slope tends towards zero (Hasannin *et al.* 1998).

4.2 RESULTS

4.2.1 Sequence details

Partial sequence data for both 16S and cytochrome *b* was obtained from a total of 63 samples (including two outgroup taxa), in which 38 were from the same individuals, and the remaining sequences from different individuals (Appendix 4.1.1). In total, 16S sequences were obtained from 60 taxa (Appendix 4.2.1a), and cytochrome *b* sequences from 40 taxa (Appendix 4.2.1b).

Sequences of the cytochrome *b* gene were compared with published sequences of *H. signifer* (Sezaki *et al.* 1999), particularly to check codon position. The DNA sequence data of cytochrome *b* translated into 106 amino acids (Appendix 4.2.1b). However, following Lydeard and Roe (1997), amino acid sequence data was not used for phylogenetic inferences, as knowledge obtained from studying the patterns of nucleotide substitutions within and among the three codon positions allows for a more robust analysis.

Each species was sequenced from at least two representative samples (if available), with additional samples of the same species sequenced to represent their different geographic localities (*H. chaophraya, H. fai, H. gerrardi ,H. granulata, H. jenkinsii, H. signifer, H. toshi, H. uarnacoides, H. uarnak, H. undulata, H.* sp. A), as well as those exhibiting varying colour morphs (*H. gerrardi, H. toshi, H. uarnak, H.* sp. A). Species represented by more than one sample were distinguished by a number after the species name (Appendix 4.1.1). Several of the samples were also indicated with a question mark before the species name, i.e. ?*H. gerrardi* 7 to 10 (Appendix 4.1.1). The placement of a question mark was to indicate insufficient available information to correctly verify sample identity. This was necessary after the discovery of several morphologically distinct 'gerrardi' subgroups within the larger 'uarnak' complex (see Chapters 2 and 5).

The 16S and cytochrome *b* sequences were 606 and 318 base-pairs (bps) in length respectively. Within the 16S sequence data set, 59 bps were situated within alignment-ambiguous regions (grey columns in Appendix 4.2.1a). These were excluded from subsequent analyses, leaving a remaining 547 bps in the 16S sequence data set. The number of variable characters in both sequence data sets represented less than half of the total respective sequence length. Within the variable characters however, the number of phylogenetically informative characters was high, representing up to 80% of the variable characters (Table 4.2.1).

Table 4.2.1. Summary of variable and phylogenetically informative character content for the partial 16S and cytochrome *b* sequences.

Gene (sequence length base-pairs)	Number of variable characters	Number of phylogenetically informative characters within the variable characters
16S (547 bps[a])		
gaps as missing	163 (30%)	128 (78%)
gaps as fifth base	195 (36%)	154 (79%)
cytochrome *b* (318 bps)		
gaps as missing	133 (42%)	112 (81%)

[a] sequence length excluding alignment-ambiguous regions.

An analysis of the mean nucleotide composition of both genes found that adenine occurred at the highest frequency in 16S, and thymine in cytochrome *b*, while guanine at the lowest frequency in both genes (Figure 4.2.1). Nucleotide composition with regard to codon position in cytochrome *b* (Figure 4.2.2, average frequency shown) indicated relatively equal frequencies (ranging between 19-30%) in first position, and a highly biased frequency in the second and third positions, with thymine being at the highest frequency in second position (41%) and cytosine in third position (36%). Guanine composition is particularly lowest in the third position, and entirely absent from two taxa (*H. chaophraya* 3 and 4).

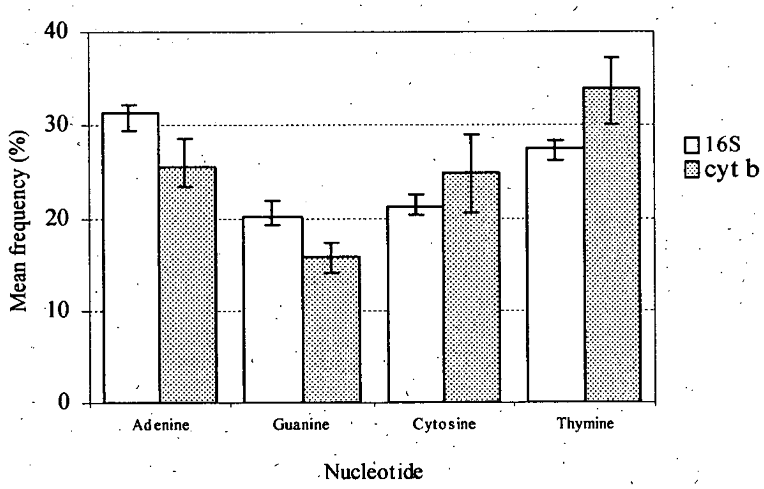

Figure 4.2.1. Mean nucleotide composition within a 547 bps region of the 16S (58 taxa) and 318 bps region of the cytochrome *b* (38 taxa) genes. Corresponding range indicated.

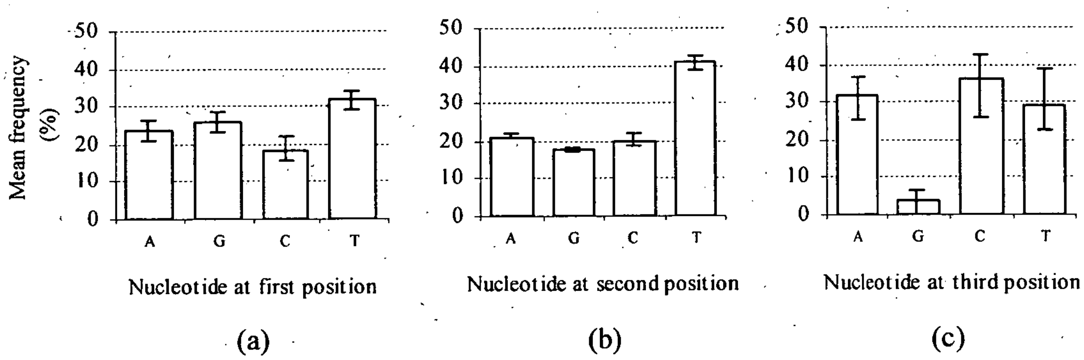

Figure 4.2.2. Mean nucleotide composition within a 318 bps region of the cytochrome *b* gene (38 taxa). a) first position, b) second position, c) third position. Corresponding range indicated. A=Adenine, G=Guanine, C=Cytosine, T=Thiamine.

The saturation of transition (Ti) substitutions in both 16S and cytochrome *b* is indicated by the reduction of their observed rate of accumulation relative to transversion (Tv), especially in ingroup and outgroup comparisons (Figures 4.2.3a,b). Squared regression coefficient (R^2) values for comparison between ingroups, and comparison between ingroup and outgroup are 0.34 and 0.09, and 0.20 and 0.36, for 16S and cytochrome *b*, respectively. Relatively low R^2 values are an indication of transition saturation. Within cytochrome *b*, the majority of nucleotide substitutions are observed at the third codon position, which is dominated by transition substitutions (Figure 4.2.4). Transversions at the second codon position are almost negligible with a low frequency of 33.

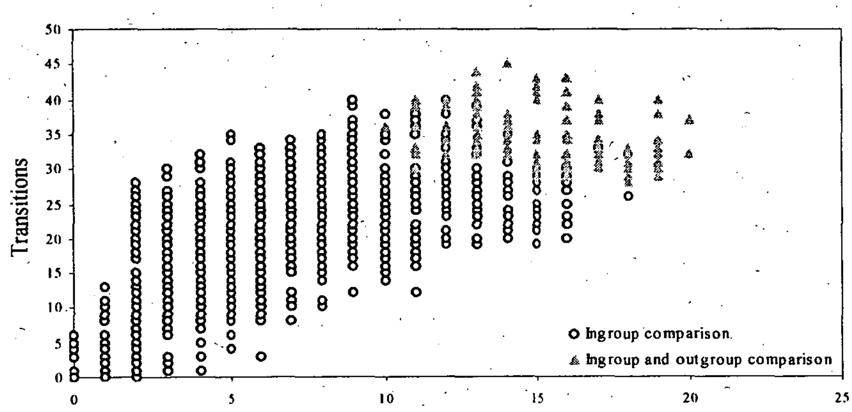

Figure 4.2.3a. Frequency of observed transition and transversion nucleotide substitutions during pair-wise comparisons of partial 16S DNA sequences. Comparisons were performed among the ingroups (circles) (R^2=0.34), and between the ingroups and the outgroups (triangles) (R^2=0.09).

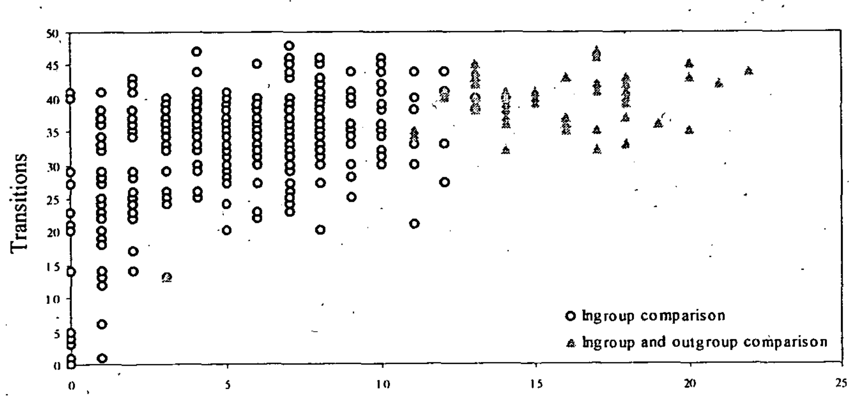

Figure 4.2.3b. Frequency of observed transition and transversion nucleotide substitutions during pair-wise comparisons of partial cytochrome *b* sequences. Comparisons were performed among the ingroups (circles) (R^2=0.20), and between the ingroups and the outgroups (triangles) (R^2=0.36).

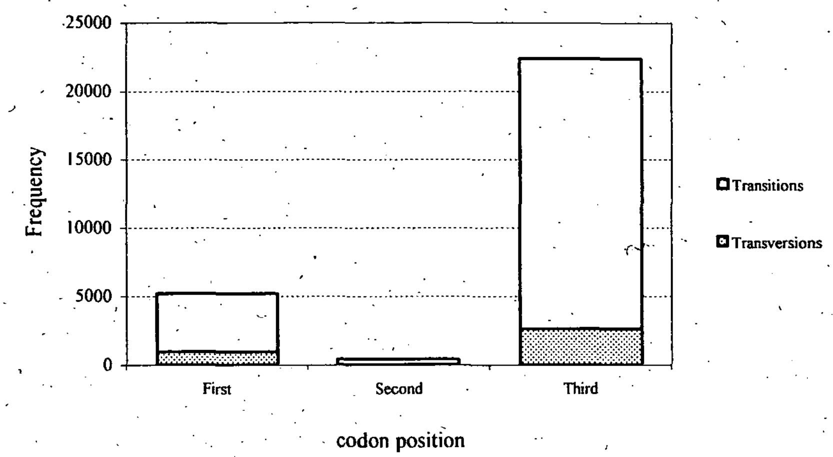

Figure 4.2.4. Frequency of observed transition and transversion nucleotide substitutions at first, second and third codon positions during pair-wise comparisons among ingroup (38 taxa) cytochrome *b* sequences.

Saturation patterns for both 16S and cytochrome *b* based on the absolute number of Ti and Tv versus HKY85 (Appendix 4.2.2a,b) and uncorrected 'p' distances (Appendix 4.2.3a,b) show virtually identical trends. Thus, only the trend for uncorrected 'p' distances is shown (Figures 4.2.5 and 4.2.6). Pair-wise sequence comparisons using both distances reveal a clear demarcation between Ti and Tv, and a relatively strong linear correlation between nucleotide substitutions (Ti, R^2=0.92 and Tv, R^2=0.72 for 16S; Ti, R^2=0.86 and Tv, R^2=0.54 for cytochrome *b*) and the distance values.

The low rate of increase in the linear correlation for Ti substitutions, however, (as indicated by a high accumulation of Ti relative to distance measure) indicates that Ti may not provide reliable phylogenetic information due to site saturation. For 16S, the reduced rate is observed at approximately 2%, and at approximately 5% for cytochrome *b*. The accumulation of transitions to transversions as derived from pair-wise comparisons was approximately 2:1 in 16S, and 6:1 in cytochrome *b*.

Nucleotide substitution analyses at each codon position using pair-wise HKY85 distance and uncorrected 'p' distance are shown in Appendices 4.2.4 and 4.2.5. Distance values were also essentially similar using either distance measure (HKY85 or uncorrected 'p') when codon position was not taken into consideration (Appendix 4.2.2b and 4.2.3b).

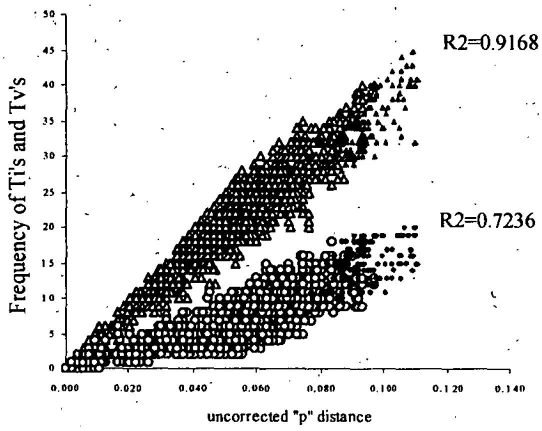

Figure 4.2.5. Frequency of observed transition and transversion nucleotide substitutions during pair-wise comparisons of partial 16S DNA sequences versus uncorrected 'p' genetic distance. Comparisons were performed among the ingroups (open triangles and open circles) and between the ingroups and outgroups (closed triangles and closed circles). Transitions are triangles, transversions are circles. R^2 values (of linear regression for the entire data set) are shown.

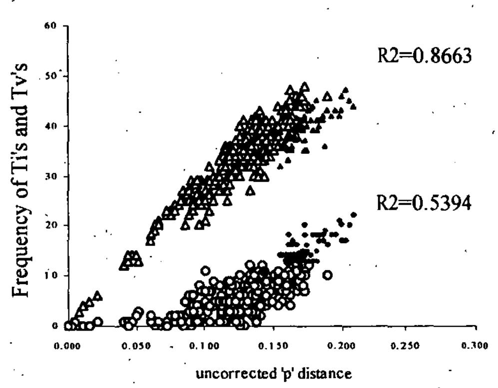

Figure 4.2.6. Frequency of observed transition and transversion nucleotide substitutions during pair-wise comparisons of partial cytochrome *b* DNA sequences versus uncorrected 'p' genetic distance. Comparisons were performed among the ingroups (open triangles and open circles) and between the ingroups and outgroups (closed triangles and closed circles). Transitions are triangles, transversions are circles. R^2 values (of linear regression for the entire data set) are shown.

Based on saturation plots of pair-wise comparisons using uncorrected 'p', the separation between Ti's and Tv's is relatively clear at codon positions 1 and 3, although at codon position 2, the separation is less clear (Figure 4.2.7). Both Ti's and Tv's are essentially linear at all codon positions, although the rates are substantially reduced beyond a certain point (distance), indicating the occurrence of saturation. At first positions, the rate of increase is reduced beyond approximately 4% in both substitution types (Figure 4.2.7a,b). At third positions, the rate of increase is reduced beyond approximately 20% in both substitution types (Figure 4.2.7e,f). All pair-wise comparisons with the outgroup taxa also indicated saturation (closed triangles in Figure 4.2.7) at larger distances.

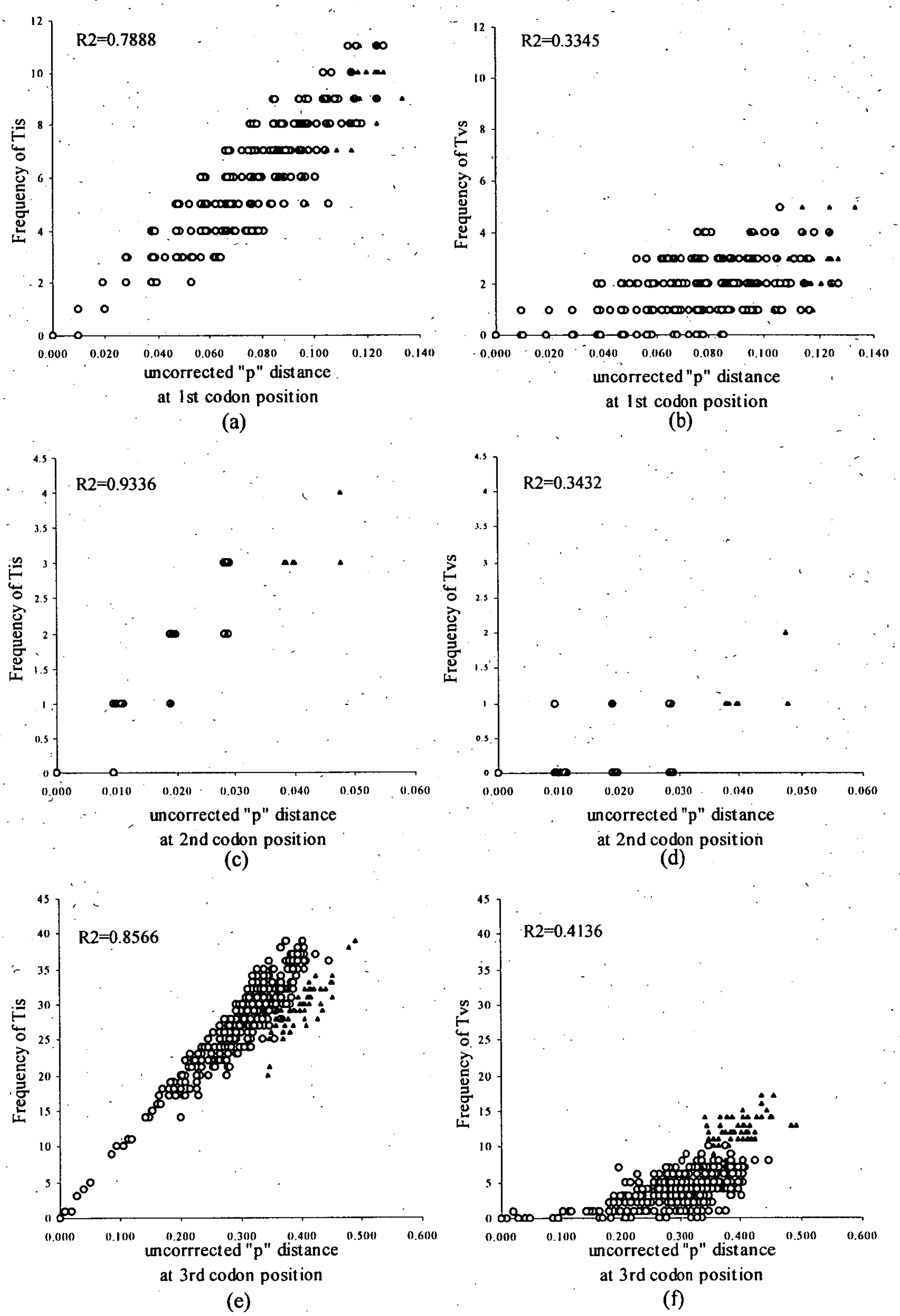

Figure 4.2.7. Frequency of observed transition and transversion nucleotide substitutions during pair-wise comparisons of partial cytochrome *b* DNA sequences versus uncorrected 'p' distance at each codon position. a-b) first codon, c-d) second codon, e-f) third codon. Comparisons were performed among the ingroups (open cirles) and between ingroups and outgroups (closed triangles). R^2 values are shown.

Therefore, saturation patterns of the first and third codons were taken into account by differential weighting of substitutions in the phylogenetic analyses. The accumulation of transitions to transversions as derived from codon pair-wise comparisons was approximately 3:1 in first positions, and 9:1 in third positions.

Pair-wise comparisons for 16S and cytochrome *b* plotted against HKY85 and uncorrected 'p' genetic distances (Appendices 4.2.2 – 4.2.5) revealed the absence of intraspecific sequence variation in several species for both genes. However, equal values of interspecific sequence divergence were detected for both data sets.

Estimates of the sequence divergence between outgroup and ingroup lineage's for 16S, ranged from 0.082 (between *H. pacifica* and *H.* sp. F) to 0.122 (between *H. pacifica* and *H. undulata* 2). However, the genetic distance values between *H. pacifica* and two other *H. undulata* sequences (*H. undulata* 1 and *H. undulata* 3) were lower at 0.103 and 0.107 respectively. Sequence divergence among ingroup taxa (including samples of the same species) ranged from 0 (found between several species pairs, i.e. *H.* sp. A 1 and 4; *H. gerrardi* 2 and 5; *H. gerrardi* 3 and 4; and *H. signifer* 2 and 3) to 0.105 (found between two species pairs, i.e. *H. signifer* 2 and *H. chaophraya* 1; and *H. signifer* 3 and *H. chaophraya* 1). Excluding samples of the same species, the least sequence divergence among ingroup taxa was 0.002 (between *H. signifer* 1 and *H. oxyrhyncha*).

Estimates of the sequence divergence between outgroup and ingroup taxa for cytochrome *b* ranged from 0.142 (found between *H. pacifica* and all three samples of *H. granulata*) to 0.210 (between *H. schmardae* and *H. pastinacoides*). Sequence divergence among ingroup taxa (including samples of the same species) ranged from 0 (found between several species pairs, i.e. *H. uarnak* 2 and 3; *H.* sp. A 1 and 2; *H.* sp. A 1 and 4; *H.* sp. A 1 and 5; *H.* sp. A 2 and 4; *H.* sp. A 2 and 5; *H.* sp. A 4 and 5; *H. gerrardi* 1 and 5; *H. toshi* 1 and 2; *H.* sp. E 1 and 2; *H. chaophraya* 3 and 4; and *H. granulata* 2 and 3) to 0.177 (between *H.* sp. F and *H. gerrardi* 1; and *H.* sp. F and *H. gerrardi* 5). Excluding samples of the same species, the least sequence divergence among ingroup taxa was 0.061 (found between *H. uarnak* 8 and *H. undulata* 3).

4.2.2 Phylogenetic signal and congruency

Both 16S and cytochrome *b* sequence data sets contained phylogenetic signal, as evident from the significant left skew of the estimated tree length-frequency distribution (graph generated by PAUP* not shown), with skewness test statistic values of g_1= -0.695, *P*<0.01 for 16S, and g_1= -0.495, *P*<0.01 for cytochrome *b*.

The partition homogeneity test indicated incongruence between the 16S and cytochrome *b* genes (*P*=0.01). Consequently, based on this result, all subsequent analyses were run separately for each data set. A further analysis of the data set later revealed the presence of a pseudo-gene, i.e. the cytochrome *b* sequence data of *H. jenkinsii*, and which was subsequently removed from the data set (data not shown).

4.2.3 Phylogenetic inference

4.2.3.1 Parsimony analysis

The level of resolution obtained in the resultant tree topologies for 16S and cytochrome *b* was dependent upon the weighting scheme employed. Weighted (differential) Ti:Tv parsimony analyses of the DNA sequences generally yielded a structurally better phylogeny which was comparable to a morphologically based phylogeny. Consequently only trees resulting from weighted Ti:Tv analyses are presented (Figures 4.2.8 – 4.2.10). The summary of tree scores for all competing trees, i.e. tree length, and indices (consistency index, CI; retention index, RI; rescaled consistency index, RC) using various weighting schemes for both 16S and cytochrome *b* are shown in Appendix 4.2.6.

In most cases, the relationships between congeneric species were well resolved (70-100% bootstrap support), although relationships between those within a larger complex (see also Chapters 2 and 3) was less well resolved (0-66% bootstrap support), and all deeper relationships between these larger complexes entirely unresolved (0% bootstrap support).

The three species complexes, i.e. '*uarnak*', '*uarnacoides*' and '*signifer*' complexes, as hypothesized based on morphological phylogeny are indicated with I, II and III respectively on each tree (Figures 4.2.8 – 4.2.10).

Parsimony analyses of the cytochrome *b* sequences using differential Ti:Tv weighting of the entire sequence resulted in four equally parsimonious trees, and a single most parsimonious tree for Ti:Tv weighting at third codon (Appendix 4.2.6). The strict consensus tree and the single most parsimonious tree resulted in similar branching patterns (Figures 4.2.9 and 4.2.10), with a substantial increase in overall structural resolution of ingroup relationships in the latter.

An indication of sample locality in the tree topology (Figure 4.2.10), further clarifies the closer relationship observed between several congeneric species, i.e. between the two *H. chaophraya* from Borneo (Malaysia) and the two *H. chaophraya* from Australia, or between the three *H. uarnak* from Borneo and the two *H. uarnak* from New Guinea region (Papua New Guinea-Irian Jaya).

The positioning of 4 questionable taxa (*?H. gerrardi* 7-10) within a clade of their assumed identity (Figures 4.2.8 – 4.2.10), confirms the suspicion regarding problems with their identification. That is, as these species represent members of a cryptic species group that are not well described, their correct identity was treated as unconfirmed because of insufficient accompanying information. (This is assessed in Chapter 5).

4.2.3.2 Pair-wise distance analysis

Pair-wise comparisons using HKY85 distance for the partial 16S sequences resulted in a single minimum evolution tree (tree score 0.64) (Figure 4.2.11), and 15 equally parsimonious trees for partial cytochrome *b* sequences (Figure 4.2.12). Branch support for congeneric species was similar (52-100%) to the trees generated by maximum-parsimony analysis, but as with maximum-parsimony trees, there is no branch support for deeper relationships between complexes.

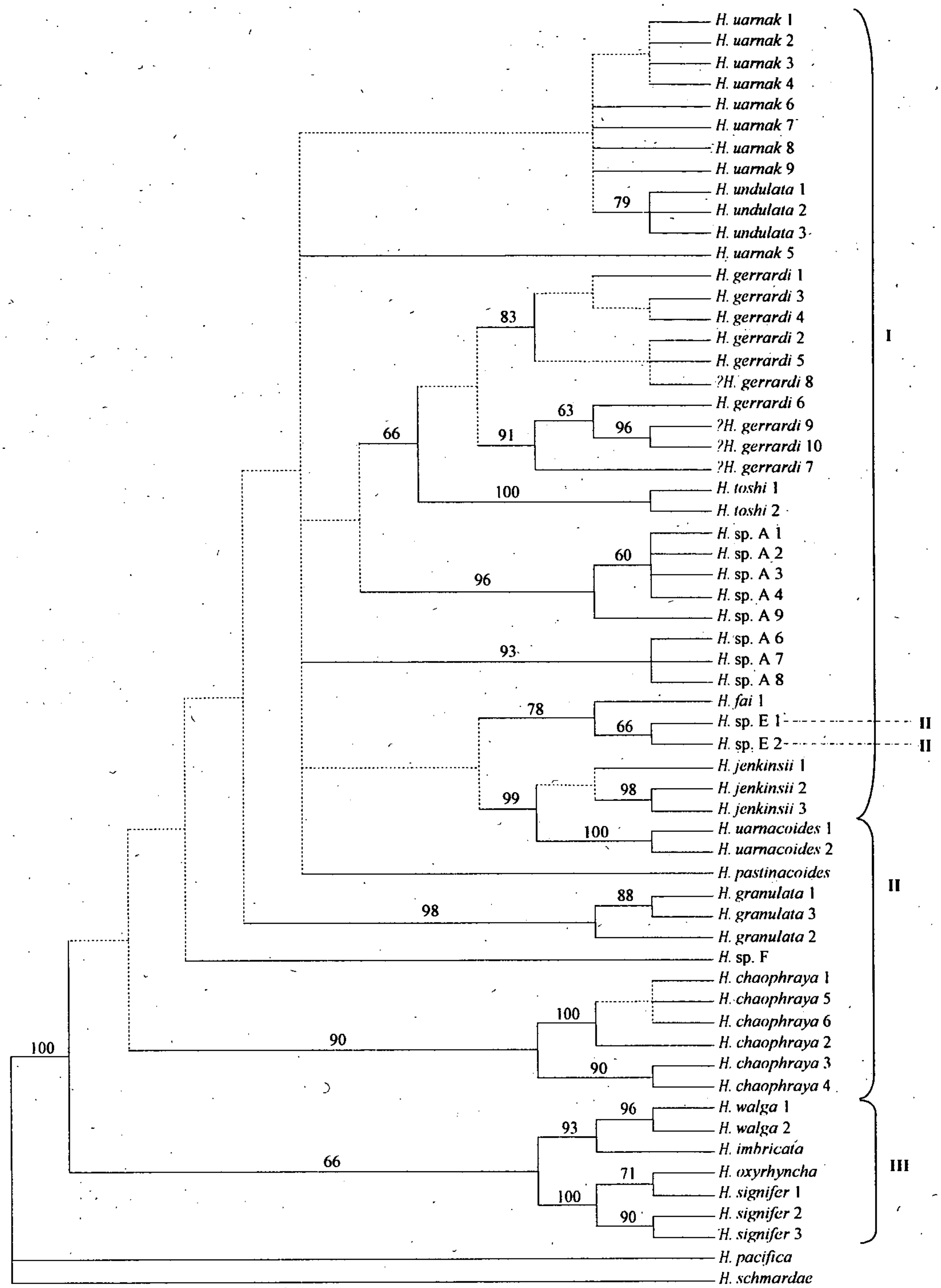

Figure 4.2.8. Strict consensus tree (tree length=484 steps, CI=0.52, RI=0.77, RC=0.41) of weighted parsimony analysis (Ti:Tv, 2:1) of partial 16S sequence data set (60 taxa, including two outgroups *H. pacifica* and *H. schmardae*). Numbers above solid branches indicate support of ≥ 50% from 2000 replicates using fast step-wise addition. Broken lines indicate lack of at least 50% bootstrap support. I='uarnak' complex; II='uarnacoides' complex; III='signifer' complex.

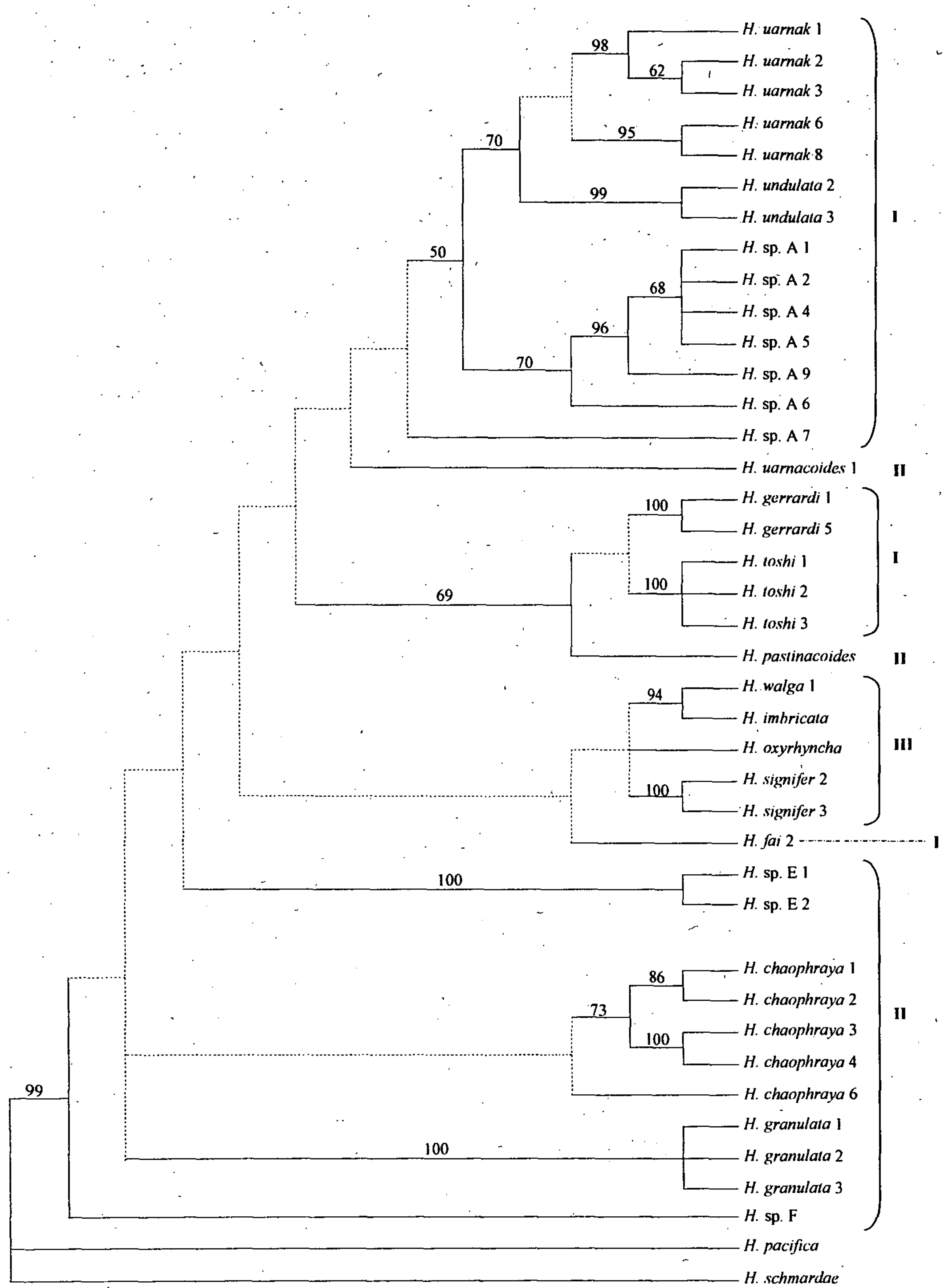

Figure 4.2.9. Strict consensus tree (tree length=770 steps, CI=0.51, RI=0.73, RC=0.37) of weighted parsimony analysis (Ti:Tv, 6:1) of partial cytochrome *b* sequence data set (40 taxa, including two outgroups *H. pacifica* and *H. schmardae*). Numbers above solid branches indicate support of ≥ 50% from 2000 replicates using fast step-wise addition. Broken lines indicate lack of at least 50% bootstrap support. I='uarnak' complex; II='uarnacoides' complex; III='signifer' complex.

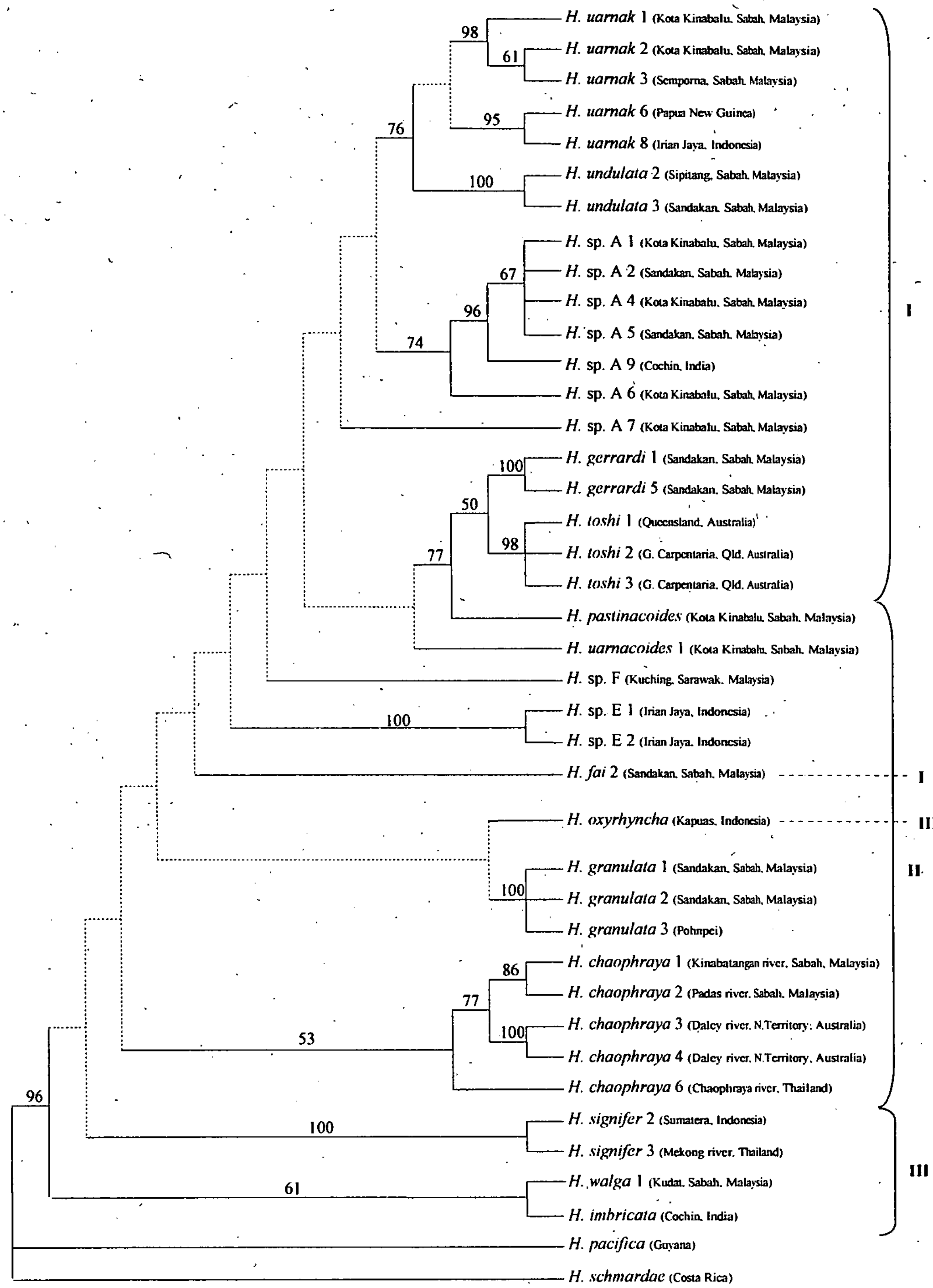

Figure 4.2.10. A single most parsimonious tree (tree length=817 steps, CI=0.50, RI=0.73, RC=0.36) of weighted third codon parsimony analysis (Ti:Tv, 9:1) of partial cytochrome *b* sequence data set (40 taxa, including two outgroups *H. pacifica* and *H. schmardae*). Numbers above solid branches indicate support of ≥ 50% from 2000 replicates using fast step-wise addition. Broken lines indicate lack of at least 50% bootstrap support. Sample locality indicated in parentheses. I='uarnak' complex; II='uarnacoides' complex; III='signifer' complex.

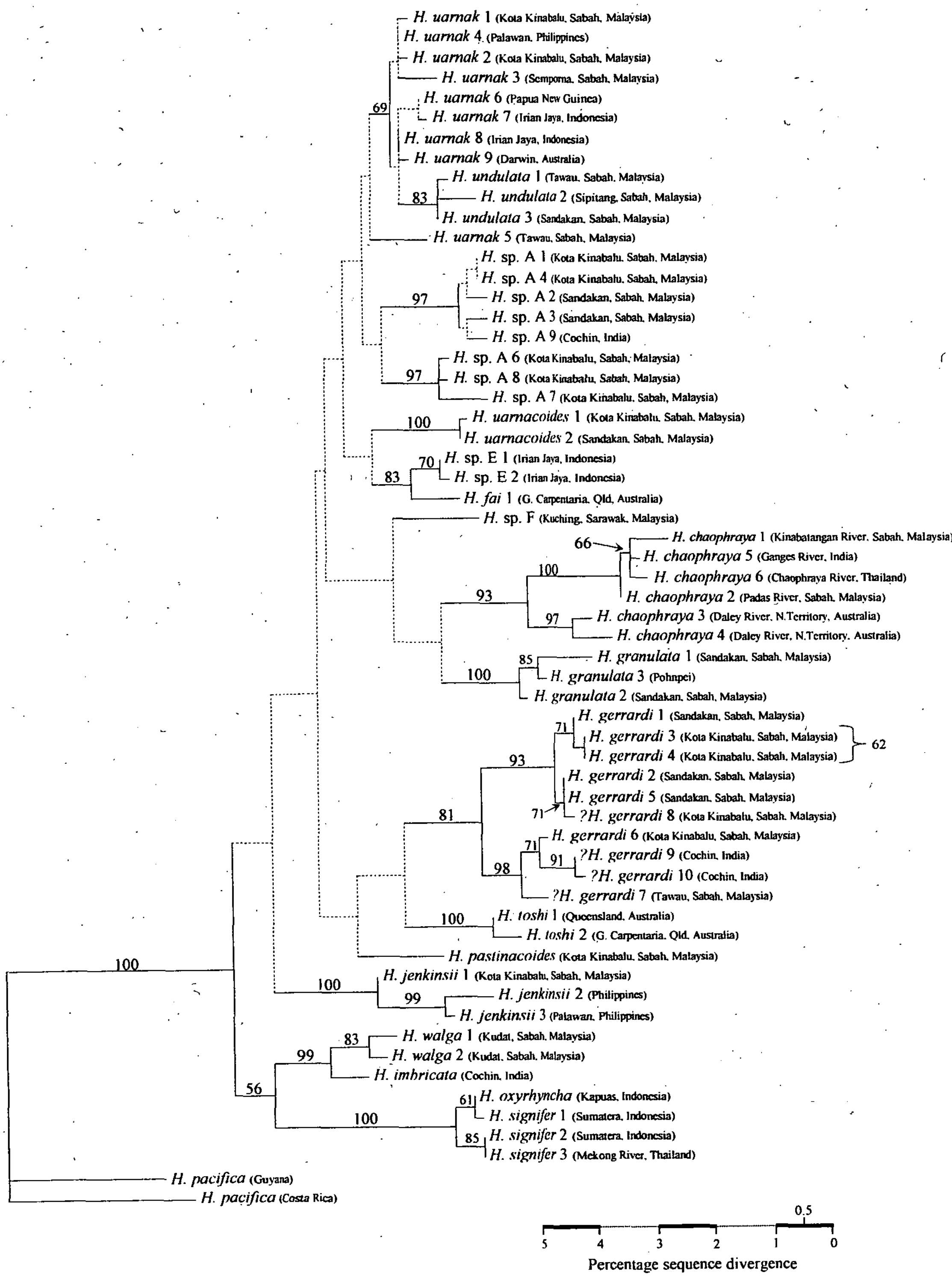

Figure 4.2.11. A single minimum evolution tree (tree score=0.64) resulting from distance analysis (HKY85) of partial 16S sequence data set (60 taxa, including two outgroups *H. pacifica* and *H. schmardae*). Branch lengths are proportional to sequence divergence as indicated by the scale bar. Numbers above solid branches indicate bootstrap support of ≥ 50% from 2000 replicates using fast step-wise addition. Where branch lengths are too short to indicate support, these are indicated with an arrow, or a right brace. Broken lines indicate lack of at least 50% bootstrap support. Sample locality indicated in parentheses.

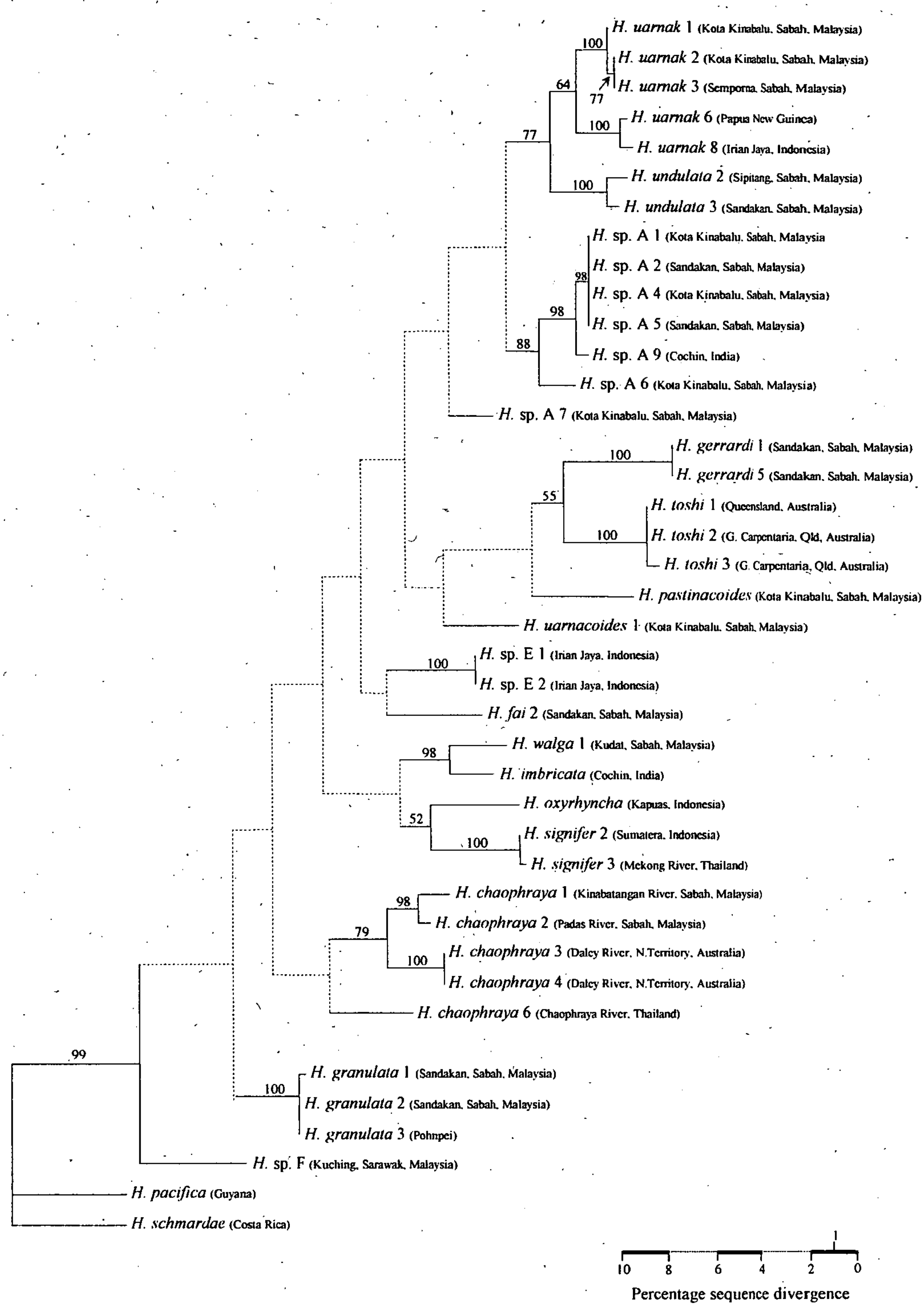

Figure 4.2.12. Strict consensus minimum evolution tree (tree score=1.37) resulting from distance analysis (HKY85) of partial cytochrome *b* sequence data set (40 taxa, including two outgroups *H. pacifica* and *H. schmardae*). Branch lengths are proportional to sequence divergence as indicated by the scale bar. Numbers above solid branches indicate bootstrap support of ≥ 50% from 2000 replicates using fast step-wise addition. Arrow indicates support where branch length is too short. Broken lines indicate lack of at least 50% bootstrap support. Sample locality indicated in parentheses.

4.3 DISCUSSION

The phylogenetic trees produced by maximum-parsimony and distance analyses of the mtDNA sequences based on 16S (Figures 4.2.8 & 4.2.11) and cytochrome *b* (Figures 4.2.9, 4.2.10 & 4.2.12) show a well resolved (70-100% bootstrap support) relationship between congeneric species. The trees however, do not show a taxonomic congruence with the morphologically-based tree generated in Chapter 3, as confidence levels tended toward zero closer to the base of the phylogeny, resulting in no support for the deeper phylogenetic relationships amongst the taxa. Nevertheless, as with the morphological-based phylogeny, the resulting topologies indicate a pattern of species subgroups or complexes within *Himantura*.

It has been shown that the number of characters used, strongly influence bootstrap values (of a phylogenetic tree) (e.g. McCracken & Sheldon 1998; Bremer *et al.* 1999; De Queiroz *et al.* 2002). According to these studies, bootstrap values are strongly influenced by the number of characters, and that the percentage of supported nodes within a tree is positively correlated with the number of characters and negatively correlated with the number of taxa. Bremer *et al.* (1999) further outlined the conditions of how a support value of 95% for all nodes might be achieved; the minimum number of characters would be three times as many as the number of nodes- with no homoplasy, with an even distribution of characters on the tree, and binary characters.

The problem of placement of *H. fai* as observed from the morphological-based phylogeny (Chapter 3), is also observed in the molecular-based phylogeny of the present study. However, the relationships of these taxa based on molecular phylogeny is considered less reliable compared to morphological-based phylogeny due to the low level of congruence among the different trees of both sequence data sets (16S and cytochrome *b*). According to Kraus and Brown (1998), such problems might be contributed to by long-branch attraction or spurious base-compositional similarity among taxa. However, the fact that the clustering of taxa is not based on branch length similarities (Figures 4.2.11 & 4.2.12), and that orthologous gene sequences are being compared (see Section 4.1.3), suggest neither of these factors are of any influence in the present phylogenetic conclusions. On the other hand, the lack of a conclusive resolution is attributed to insufficient phylogenetic signal from the individual mtDNA sequences used (e.g. Flook *et al.* 1999; Joy & Conn 2001) due to sequence saturation (see Results). Most recently, the phylogenetic utility of the mtDNA control region (CR) sequence appears as a better option for elucidating congeneric relationships (Takahashi & Goto 2001). Comparisons of sequences among vertebrates have shown that both relatively fast and slowly evolving areas (of mutation rate) lie within the mtDNA CR (Lee *et al.* 1995 *in* Takashi & Goto 2001).

Estimates of sequence divergence between outgroup and ingroup taxa, and among ingroup taxa for both genes tended to be low, in some cases zero sequence divergence between species pairs. Although sequence divergence values can not be used for assessing species status, these values may give an idea of relative distances among the taxa analysed when used in conjunction with diagnostic (morphological) characters (e.g. Hackett 1996).

Overall, the homologous region of partial sequence data of the 16S gene was less conserved compared with that of cytochrome *b* gene, although the sequenced length was almost twice as long as in the latter. This is attributable to the unexpected presence of two alignment-ambiguous regions in 16S, involving almost 10% of the total number of nucleotides. As for the cytochrome *b* gene, the sequenced region apparently involved the more conserved region within the gene (e.g. Lydeard & Roe 1997). This, and the aforementioned factors all contribute to the low or absence of support particularly for deeper relationships among the taxa.

Interrelationship among cryptic species

The clustering of cryptic species, i.e. species exhibiting an array of colour pattern in the same, or different life-stages, which in this case are the *H. gerrardi, H. toshi, H. uarnak, H. undulata* and *H.* sp. A, with relatively high ($\geq 70\%$) bootstrap support is particularly helpful in discerning their interrelationship, which otherwise is not possible based on (the currently available) morphological data alone.

The problem of misidentification of Indo-Pacific stingrays with dark spotted or reticulated colour patterns was highlighted by Last and Stevens (1994), in which they particularly remarked the name *Himantura uarnak* as having been used for several similar species. Confusion regarding species identification stems from the assumption that individual adult rays are capable of altering their colour pattern to match the substrate, they noted. Analyses of unpublished information comprised mainly of colour prints in the collection of P. Last (pers. comm.), as well as from personal observations during field samplings, revealed that species indeed display a rather distinct colour patterning, although however, more subtle differences in colour morphs were observed among conspecific adults, or large individuals (>500 mm disc width). Transformation of colour pattern from spots to reticulation particularly in *H. uarnak*, *H. undulata* and *H.* sp. A, is observed to be an ontogenetic character.

On the other hand, colour patterns of *H. gerrardi* and *H. toshi* usually remain as spots even in adults, the former with white spots and the latter with darker (usually dark brown to blackish) spots, but rarely with pale to whitish fuzzy spots. In *H. gerrardi*, the spots rarely transform into crescentic shapes in adults, whilst in *H. toshi*, the spots sometimes transform into a floral pattern, with smaller white spots arranged around each (larger) dark spot. Both species were observed displaying uniform plain disc (no spotting), or spots confined to the posterior half of the disc, but in any case, the tail is always banded.

It should be noted that two forms of *H. gerrardi*, based on the shape of the mid-scapular denticle (Chapter 5) were observed during this study. The two forms, tentatively termed 'small denticle', and 'large denticle' however, were detected only later (after field sampling), and only then was it discovered no tissue samples of the latter form were obtained for molecular analysis. Unlike the reticulated stingrays, the colour patterns of the two *H. gerrardi* forms are rather indistinct, i.e. both forms displaying varying degrees of white spotting, and the tails banded even in adults. Moreover, the discovery of several new species (i.e. *H.* sp. B-D; Chapters 3 & 5) based on the examination of materials previously identified as *H. gerrardi* from Saudi Arabia and Pakistan, and their close relationship based on morphological data

(Chapter 3) suggests that the name, as for *H. uarnak*, has also been used for several similar species. This finding serves to demonstrate further, the poor taxonomic knowledge of the Indo-Pacific *Himantura*.

Thus, as mentioned earlier, confirmation of the close-relatedness among cryptic species is otherwise not possible, based on the limited available morphological data alone. A major difficulty in working with stingrays is herein reiterated, that the large size which the adults may reach, posed a major limitation on the number of specimens that could be collected within the relatively short sampling period of this study. Hence the reason, 'available data' for the cryptic taxa (in this study) usually means only colour print photographs indicating the pattern of the dorsal surface is available.

Biogeographical patterns

The close phylogenetic relationship between putative conspecifics of widespread species and of more restricted species supported by high bootstrap values (Figures 4.2.11 & 4.2.12), offers further insight into their possible historical biogeography. The widespread species include several of the cryptic taxa described earlier. These have been recorded from throughout the Indian Ocean to the Western Pacific Ocean of the Indo-Pacific region. On the other hand, the more restricted species (i.e. *H. chaophraya*, *H. signifer*) primarily refers to freshwater populations inhabiting landlocked areas within the region.

The close relationship among the latter group, which included disjunct populations of *H. chaophraya* from continental Asia (Ganges River, India and Chao Phraya River, Thailand), Borneo (Padas and Kinabatangan Rivers in Sabah), and Australia (Daley River) though not unexpected, presents strong evidence to support arguments regarding their hypothesized affinities as based on limited morphological evidence. Based on available data, both morphometric and meristic characters are overlapping in their range, and only subtle differences in morphological characters (i.e. disc shape, angularity of the snout tip, and markings on the ventral surface of the disc) were observed (Chapter 5). The differences in mtDNA and amino acid sequences of complete cytochrome *b* between *H. chaophraya* populations from

India and Thailand, were also observed by Sezaki *et al.* (1999), in which they implied allopatric speciation might have taken place.

Combined with the fact that freshwater and estuarine species occupy a basal position in the present phylogeny (see also Chapter 3), lends support to the hypothesis of multiple colonizations into fresh water by dasyatid species (Compagno & Cook 1995). The present distribution of these geographically isolated populations further suggests species need not have dispersed through marine habitats, as hypothesized by Compagno and Roberts (1982) for the scattered populations of *H. signifer* they described. This finding in particular supports the theory that the East and Southeast Asian continental terranes originated on the margin of India - North and Northwestern Australia of the ancient Gondwanaland (Metcalfe 1998). Moreover, an examination of the substructure of the Indo-Pacific chondrichthyan fauna by Last and Séret (1999) led them to hypothesize the faunal origins of the Australasian region as having evolved in the Indo-West Pacific rather than in central and eastern Pacific.

4.4 CONCLUSION

The sequenced taxa represent most of the extant species currently assigned as *Himantura*, following a taxonomic review of the genus (Chapters 2 and 5). The results presented here are a conservative estimate of their phylogenetic relationships, and are generally congruent with the morphological-based phylogeny (Chapter 3). Nucleotide sequence data is useful in elucidating the relationship among cryptic taxa, and the comparison of whipray fauna between different subregions within the Australasian region as well as between different localities within the greater Indo-West Pacific region reveal these geographically isolated freshwater populations as conspecifics. Most notably, the findings of present study have led to the detection of ontogenetic development of colour pattern and the discovery of key diagnostic characters involving squamation, for the cryptic species. Understanding the ontogeny of colour pattern combined with squamation characters, reveal that juveniles belonging to this complex (i.e. uarnak complex) are not necessarily more different from each other than the adults, as suggested by Last and Stevens (1994).

Suggestions for future studies include the sequencing of additional genes (e.g. Takahashi & Goto 2001), particularly to resolve the deeper relationship among ingroup taxa. Inclusion of more species, which ideally would include the complete species on the list, could better improve the resulting phylogeny (e.g. Bremer *et al.* 1999). It should also be noted that the best result (tree) for cytochrome *b* was obtained by differential weighting of characters. This analytical method is proposed when dealing with other protein coding regions such as cytochrome oxidase I and II.

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CHAPTER 5

5.0 TAXONOMIC ACCOUNTS

Since Nelson (1994), the most updated systematic accounts of rays (and sharks), incorporating findings of recent phylogenetic studies is presented by Compagno (1999a, b). Over 62 species of whip-tailed stingrays (Family Dasyatidae) grouped into 5 or 6 genera are recognized. The most significant change in this account is the reassignment of two marine amphi-American *Himantura*, and three Eastern Hemisphere *Taeniura* to the Family Potamotrygonidae (river stingrays) (Compagno 1999b). Questions remain, however, about the potential validity of several putative species and how species groups with unique body forms within *Himantura* are related. The reliability of many early revisions are much in doubt as these were influenced by the absence of representative material of each species, and the poor appreciation of diversity of the group (Last 1979).

Nomenclatural issues

A major source of confusion in stingray taxonomy lie in the way some authors liberally changing and utilizing the nomenclatural status of some genera, and not adhering to the outlines of the *'International Code of Zoological Nomenclature'* (ICZN 1999). For example, Garman (1913) in his classification of the stingrays subdivided them into subgroups, and explicitly stated *'for convenience'* the species of this genus (*Dasybatus*) may be arranged by means of the cutaneous folds on the tail in four more or less distinct groups. This he introduced without any phylogenetic reference, but in the following years, some of the subgenera he introduced have been followed through in recent phylogenetic reconstruction of higher level (stingray) systematics (e.g. Nishida 1990), and has seen an upgraded status to become genus (e.g. Rainboth 1996).

In the literature, Dasyatidae is sometimes spelled Dasyatididae, the latter spelling recommended as the grammatically correct family-group name (Steyskal 1980) of the more established former spelling. Some taxonomists (e.g. Last & Stevens 1994) adhered to this recommendation, while ignored by others (e.g. Compagno 1999a, b, c), resulting in both spellings being observed in the current literature. Steyskal's recommendation thus, unfortunately, caused further confusion in stingray nomenclature, especially for the non-taxonomists (e.g. students, fisheries biologists, and marine conservationists among others). In this study, I adopted the spelling Dasyatidae, following Compagno (1999a, b, c; pers. comm.). Compagno's justification for retaining the old but more established spelling (pers. comm.), has now been incorporated in the latest edition of the Code (ICZN 1999; Ferraris 2000).

Extant whip-tailed stingray species

Twenty-one species of Indo-Pacific whip-tailed stingrays, including 7 new species tentatively designated as *Himantura* are recognized in this study. Originally designated based on the synapomorphy of 'absence of or rudimentary tail fold', a concurrent study on morphology-based phylogeny (Chapter 3) revealed other synapomorphies, concerning other parts of the body. These are squamation characteristics (presence of secondary denticle band) and clasper characteristics (i.e. pseudosiphon positioned on inner margin of clasper, and presence of pseudorhipidion). The close relationship between cryptic species was revealed using molecular techniques (DNA sequencing). One species, i.e. *H. marginata* is treated as *incertae sedis*, its doubtful characteristics outlined to illustrate uncertainties regarding its taxonomic placement. Valid extant members of the genus *Himantura* are as follows:

Valid extant members of the genus *Himantura*

H. chaophraya Monkolprasit & Roberts 1990
H. fai Jordan & Seale 1906
H. gerrardi (Gray 1851)
H. granulata (Macleay 1883)
H. imbricata (Bloch & Schneider 1801)
H. jenkinsii (Annandale 1909)
H. oxyrhyncha (Sauvage 1878)
H. pastinacoides (Bleeker 1852)
H. signifer Compagno & Roberts 1982
H. toshi Whitley 1939
H. uarnacoides (Bleeker 1852)
H. uarnak (Forsskål 1775)
H. undulata (Bleeker 1852)
H. walga (Müller & Henle 1841)
H. sp. A (leopard whipray)
H. sp. B (Arabian banded tail)
H. sp. C (Pakistan whipray)
H. sp. D (short-tail whipray)
H. sp. E (Hortles whipray)
H. sp. F (tube-mouth whipray)
H. sp. G (Cooks whipray)

Nominal species of Indo-West Pacific whiptailed stingray and its current placement (revised) in the *Himantura* are as follows:

Nominal species	Current placement
Raja sephen var. *uarnak* Forsskål 1775	*Himantura uarnak* (Forsskål 1775)
Raja imbricata Bloch & Schneider 1801	*H. imbricata* (Bloch & Schneider 1801)
Raia fluviatilis Hamilton-Buchanan 1822	*nomen nudum* or *nomen dubium*
?*Trigon russellii* Gray 1834	*H.* sp. A
Trygon purpurea (Smith) Müller & Henle 1841	*H. fai* Jordan & Seale 1906
Trygon walga Müller & Henle 1841	*H. walga* (Müller & Henle 1841)
Trygon variegatus McClelland 1841	*H. uarnak* (Forsskål 1775)
Trygon gerrardi Gray 1851	*H. gerrardi* (Gray 1851)
Trygon heterurus Bleeker 1852	*H. walga* (Müller & Henle 1841)
Trygon macrurus Bleeker 1852	*H. gerrardi* (Gray 1851)
Trygon maculata Kuhl & van Hasselt in Bleeker 1852	*nomen nudum*
Trygon pareh Bleeker 1852	*H. pastinacoides* (Bleeker 1852)
Trygon pastinacoïdes Bleeker 1852	*H. pastinacoides* (Bleeker 1852)
Trygon polylepis Bleeker 1852	*H. chaophraya* Monkolprasit & Roberts 1990
Trygon uarnacoïdes Bleeker 1852	*H. uarnacoides* (Bleeker 1852)
Trygon undulata Bleeker 1852	*H. undulata* (Bleeker 1852)
Trygon dadong Bleeker 1856	*H. imbricata* (Bloch & Schneider 1801)
Trygon bleekeri Blyth 1860	*H. uarnacoides* (Bleeker 1852)
Trygon ellioti Blyth 1860	*nomen nudum*
Trygon marginatus Blyth 1860	*incertae sedis*
Trygon (Himantura) nuda Günther 1870	*H. imbricata* (Bloch & Schneider 1801)
Trygon (Himantura) punctata Günther 1870	*H. uarnak* (Forsskål 1775)
Raja obtusa Ehrenberg in Klunzinger 1871	*nomen nudum*
Trygon liocephalus Klunzinger 1871	*H. fai* Jordan & Seale 1906
Trygon (Himantura) oxyrhynchus Sauvage 1878	*H. oxyrhyncha* (Sauvage 1878)
Trygon granulata Macleay 1883	*H. granulata* (Macleay 1883)
Himantura fai Jordan & Seale 1906	*H. fai* Jordan & Seale 1906
Trygon alcockii Annandale 1909	*H. gerrardi* (Gray 1851)
Trygon favus Annandale 1909	*H. undulata* (Bleeker 1852)
Trygon jenkinsii Annandale 1909	*H. jenkinsii* (Annandale 1909)
Urogymnus laevior Annandale 1909	*H. chaophraya* Monkolprasit & Roberts 1990
Trygon ponapensis Günther 1910	*H. granulata* (Macleay 1883)
Dasybatus (Himanturus) krempfi Chabanaud 1923a	*H. oxyrhyncha* (Sauvage 1878)
Dasybatis uylenburgi Giltay 1933	*H. walga* (Müller & Henle 1841)
Himantura toshi Whitley 1939	*H. toshi* Whitley 1939
Dasyatis microphthalma Chen 1948	*Dasyatis acutirostra* Nishida & Nakaya (1988a) or *nomen nudum*
Himantura signifer Compagno & Roberts 1982	*H. signifer* Compagno & Roberts 1982
Himantura draco Compagno & Heemstra 1984	*H. jenkinsii* (Annandale 1909)
Himantura chaophraya Monkolprasit & Roberts 1990	*H. chaophraya* Monkolprasit & Roberts 1990

5.1 SPECIES COMPLEXES OF THE GENUS *Himantura*

5.1.1 Definition of genus

External diagnostic characters

Small to very large species, adults between 30 and 200 cm disc width. Disc shape rhomboidal, oval, or circular; snout broad based, broadly angular to rounded at tip, and tip with or without small triangular lobe; lateral apices variably shaped from being acutely to obtusely rounded, or from acutely to obtusely angular, and tail moderately stout to slender, generally tapering to a fine point. Disc with denticles on the dorsal surface of disc and tail, forming a broad denticle band along the trunk in sub-adults and adults; thorns and tubercles appearing later, usually in large adults. Ventral surface of disc void of denticles. Trunk depressed and flattened. Tail base moderately broad to narrow, slightly compressed to cylindrical in cross section beyond sting base; length moderately elongate but usually whip-like, reaching up to 3 times disc length in most species; usually 1 to 2 stings on dorsal surface of tail at a distance well-apart from tail base; skin folds or flaps lacking (rudimentary in *H. imbricata*), but weak longitudinal keels along the tail length present in several species. Head forming part of disc, ventrally demarcated by the distance between the snout tip and fifth gill slit; snout moderately elongate (about nine times eye-length) to extremely elongate (about seventeen times eye-length). Orbits clearly demarcated from head; spiracles dorsolateral, or lateral on head. Mouth undulated and broadly arched, without prominent knobs, or depressions, labial folds prominent in one species (*H.* sp. F); upper jaw extended outward slightly at symphysis, partly overlain by lower jaw; lower jaw double convex, midline moderately indented; oronasal groove present; no enlarged sensory pores on chin. Floor of mouth usually with four well-developed oral papillae (absent in *H.* sp. E and *H.* sp. F); palate with a central longitudinal ridge and two angularly positioned longitudinal ridges of skin. Nostrils slit-like, with a flared posterior end, anterior nasal flaps medially expanded and fused into a broad, skirt-shaped, posteriorly expanded nasal curtain or internasal flap that overlaps mouth; inner posterior lobe well-developed. Oral tooth rounded-oval in shape and flat, keeled, or with short cusps on their crowns, closely-set in a band or pavement-like, crowns well separated from one another; size varying continuously lateral to symphysis, largest at or adjacent symphysis, smallest near mouth corner. Pelvic-fins rectangular, almost entirely overlapped by the pectoral-fins. Claspers of adult males moderately elongated, slightly depressed but stout; oval in cross section; apopyle on anteromediodorsal surface connected to hypopyle by an open, posteriorly curved clasper groove; clasper glans simple; dorsal lobe supported by dorsal marginal and dorsal terminal cartilages and ventral lobe by ventral marginal and ventral terminal cartilages; ventral lobe without clasper spine or associated terminal cartilage; no structure inside hypopyle; a large pseudopera laterally situated on ventral clasper lobe below hypopyle; lining of pseudopera varying from smooth to reticulated or fimbriated; pseudosiphon present on inner margin (dorsomedial surface) of clasper, its cavity lying between medial edge of covering piece, posteroventral edge of dorsal marginal cartilage, and anterodorsal edge of dorsal terminal cartilage; clasper pseudorhipidion present. Sexual dimorphism characteristics, apart from the presence of claspers and corresponding fewer number of pelvic-fin radial counts in males, i.e. sexual dental dimorphism observed in several species.

Internal diagnostic characters

Jugular component of the hyomandibular canal forming a deep lateral hook. Neurocranium with short to moderately elongate and broad nasal capsules; anterior edge of nasal capsules round to angular, medially indented; extreme postero-ventrolateral surface of nasal capsule with an oval facet for antorbital cartilage; nasal apertures transversely oval and elongate, internasal plate high and broad; fontanelle wide anteriorly, narrowing posteriorly, extending to postorbital process insertion; basal plate slightly arched in lateral view, sides slightly divergent anteriorly in ventral view; internal carotid artery foramina on lateral edges of basal plate, anteroventral of orbital fissure; efferent spiracular artery foramina below optic stalk on lateral surface of basal plate; preorbital processes short to moderately elongate, well defined from supraorbital crests; supraorbital crests low and strong, separated by deep notch from postorbital processes; postorbital processes broad, wing-like; orbital region rectangular; orbits include the optic stalk, orbital fissure, interorbital canal, foramina for the orbitonasal canal, anterior cerebral vein, and optic, oculomotor, trochlear, and palatine nerves; otic capsules short, its dorsal surface sloped ventrolaterally from sphenopterotic ridge; lateral commissure and foramen for hyomandibular nerve positioned on anterior end of otic capsule, hyomandibular facet just behind these structures not reaching occiput; occiput with broad, low, convex occipital condyles, slightly protruded at the lateral tip.

Scapulocoracoid relatively broad, and low to high; coracoid bar short and stout; lateral face sub-rectangular, with broad base tapering gently upwards and medially to narrow articular condyle at tip of scapular process; predorsal, preventral and postventral foramina large; postdorsal foramina with variable size and numbers; procondyle high and long; mesocondyle short to long, usually separated from metacondyle.

Pelvic girdle not angularly arched, parabolic in shape, moderately elongated dorsal iliac processes, a pair of small ischial processes, and three to six obturator foramina on each side; anterolateral processes smaller; prepubic processes absent.

Mixopterygium relatively simple; two basal segments connect the pelvic basipterygium to clasper axial cartilage, the first broad and wedge-shaped, the second cylindrical; axial cartilage cylindrical, arching laterally, with a slightly depressed spatulate tip reaching tips of dorsal and ventral terminal cartilages; beta cartilage, not present as a separate element, apparently represented by a long, depressed, free cartilaginous flange originating anteriorly over basal segments and merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad and subquadrate-triangular, with a truncate posterior edge, broad medial flange, and narrow lateral flange that forms the roof of the clasper groove; ventral marginal cartilage a narrow, laterally expanded plate on the axial cartilage, with a straight lateral margin forming the floor of the clasper groove; dorsal terminal cartilage large, broad, wedge-shaped, medially grooved; with a broad anterior base articulating with posterior edge of dorsal marginal, a narrow posterior end opposite tip of axial cartilage; ventral terminal cartilage large, complex, oval rectangular, and scoop-shaped; with a broad, arched lateral flange forming the roof of the pseudopera and a recurved posterolateral tip forming a partial and a recurved posterolateral tip forming a partial floor under it.

Vertebrae centra extending to before base of sting, except in members of the signifer complex, and in *H. granulata*; rod-like beyond to tail tip.

Colour

About half of the species are dull greyish, brownish, yellowish, or greenish dorsally; the other half having whitish, or blackish ocellate and reticulate patterns; most species paler ventrally, usually white. A broad dark ventral disc margin present in several species; ventral surface of *H. granulata* usually blotched, except in newborns.

Habitat, biology, and fisheries

Found throughout the Indo-West Pacific region, with specific subregional distribution. Most species are demersal, inhabiting inshore waters; a few are either obligate freshwater species, or estuarine (brackishwater) species, and the rest are euryhaline. Viviparous with litters of 1 to 2 young. Feed mostly on benthic invertebrates and small (juvenile) benthic fishes. Eighteen species occur in FAO Fishing Area 71, three other species (*H.* sp. B-D) recorded only from the west of the Area (i.e. India, Kuwait and Pakistan). Ray fisheries are important in the area with substantial landings off Indonesia, Thailand, Singapore, and Malaysia (sensu Last & Compagno 1999). In East Malaysia (Sabah and Sarawak), stingrays are the dominant ray components of the catch (pers. observation). Most species are used but information on the relative importance of each on a regional basis is poor. Since the beginning of 1999, it was observed from fish markets around Sabah, there exist an international market for the denticle band of certain stingray species (i.e. *H. gerrardi, H. pastinacoides* and *H. uarnacoides*) for making wallets (pers. observation). However, no documented information about the existence of this trade in Sabah is known to the author.

Similar genera occurring in the area

Dasyatis: disc margin anteriorly convex and posteriorly straight; posterior end of nostrils not flared; free posterior margin of nasal curtain narrower than anterior margin; tail with relatively wider and more depressed base, structurally stouter and relatively shorter in length, long dorsal and/ or ventral skin fold (rather than long and lacking a skin fold); dorsal surface of disc and tail almost entirely naked in most Indo-Pacific species, i.e. denticle band not developed even in adults.

Taeniura: disc subcircular; free posterior margin of nasal curtain rather strongly fimbriate; tail with wide, depressed base, relatively shorter in length, and with a long ventral skin fold extending to tail tip.

Pastinachus: center of disc thickened; upper and lower jaws strongly arched, tooth band on upper jaw strongly indented at symphysis; tail with wide, depressed base, relatively shorter in length, with long and broad ventral skin fold not extending to tail tip.

Urogymnus: disc subcircular; dorsal disc surface entirely covered with rough denticles; tail stout and short, lacking stings on tail.

5.1.2 Key to species complexes

1 Apices of disc more or less angular; cross section of tail base subcircular; large species ... ... **'uarnak' complex (p. 5-9)**

Apices of disc moderately to broadly rounded; cross section of tail base depressed; small to large species **2**

2 Teeth not sexually dimorphic, cusps of mature males not acute and elongate; moderate to large species; birth size more than 100 mm disc width; denticle band only beginning to develop by 300 mm disc width; marine and estuarine ... ... **'uarnacoides' complex (p. 5-160)**

Teeth sexually dimorphic, cusps of mature males acute and elongate; small species; birth size less than 100 mm disc width; denticle band well developed by 300 mm disc width; freshwater and estuarine ... ... **'signifer' complex (p. 5-243)**

5.2 'UARNAK' COMPLEX

5.2.1 Definition of complex

Large species, adults exceeding 1 m in disc width. Disc shape rhomboidal (suboval in *H. undulata*); snout angular at tip; lateral apices moderately angular; tail slender and whip-like, subcircular in cross-section at tail base and beyond sting base. Dorsal surface of disc generally with colour patterns (spots, reticulations, or ocelli) (plain in *H. fai, H. jenkensii, H.* sp. B, *H.* sp. C, and *H.* sp. D); ventral surface plain and pale. Juveniles usually with banded tail (i.e. *H. gerrardi, H. toshi, H. uarnak, H. undulata, H.* sp. A and *H.* sp. B). Teeth not sexually dimorphic, cusps of mature males not acute and elongate.

5.2.2 Key

1 Suprascapular denticle(s) present; upper surface of disc plain or with colour pattern; tail banded (with alternating whitish and brownish bands in young) and/or reticulated (in adults), or only with marbled appearance **2**

Suprascapular denticle absent (in young and adults); upper surface of disc and entire surface of tail uniformly coloured **9**

2 Upper surface of disc with patterns of spots, reticulations, or ocelli **3**

Upper surface of disc plain (uniformly coloured)... ... ... **7**

3 Pattern not dense; spots or ocelli more than diameter of the largest apart; edges of spots sometimes fuzzy, especially in adults **4**

Pattern extremely dense; spots, reticulations or ocelli less than diameter of largest marking apart; edges of markings usually sharply demarcated **5**

4 Spots whitish to yellowish; primary denticle band absent in young and adults; ... ... ***Himantura gerrardi*** **(p. 5-24)**

Spots darkish to brownish (rarely whitish); primary denticle band consisting heart-shaped denticles present in young and adults ... ... ***Himantura toshi*** **(p. 5-60)**

5 Pattern dominated by irregular spots in specimens of up to 700 mm disc width; beyond 700 mm disc width, pattern dominated by ocelli resembling the spots of a leopard; snout bell-shaped; primary denticle band consisting a row of broad heart-shaped denticles present in adolescents and adults ... ... ***Himantura*** **sp. A (p. 5-116)**

Pattern dominated by reticulations in specimens exceeding 500 mm disc width; primary denticle band absent **6**

6 Reticulations fine; smaller specimens with relatively small spots; snout triangular, anterior margin almost straight; apex of pectoral-fins narrowly rounded; 1-2 ovate to broad heart-shaped suprascapular denticles ... ***Himantura uarnak*** **(p. 5-75)**

Reticulations coarse (up to 5 times wider than the fine reticulations); smaller specimens with relatively large spots; snout narrowly triangular, anterior margin concave; apex of pectoral-fins moderately rounded; 3 pearl-shaped suprascapular denticles ... ... ***Himantura undulata*** **(p. 5-95)**

7 Suprascapular denticles small, seed-shaped; delayed squamation, denticle band along trunk and tail sparse even at 325 mm disc width, except for a row of closely set seed- and narrow heart-shaped denticles in primary denticle band; disc wider than long; dorsal half of tail weakly banded behind sting base, ventral half uniform dark-brown ... ... ***Himantura*** **sp. C (p. 5-145)**

Suprascapular denticles broad heart-shaped or pearl-shaped; rate of squamation relatively fast, denticle band along trunk well-developed by 240 mm disc width; primary denticle band obsolete by 240 mm disc width; disc about as wide as long; ventral half of tail uniform dark-brown **8**

8 Tail banded in neonates and juveniles, uniform blackish in adults; tail rugose even in young (ca. 400 mm disc width); lateral apices of disc moderately angular ... ... ***Himantura*** **sp. B (p. 5-136)**

Tail uniform dark brownish or blackish, dorsal half weakly banded behind sting or slightly marbled; tail smooth in young (ca. 400 mm disc width); lateral apices of disc narrowly rounded ... ... ***Himantura*** **sp. D (p. 5-152)**

9 Enlarged thorn-like denticles along midline of trunk and tail absent; tail whip-like, length 2.5 times disc width ... ... ***Himantura fai*** **(p. 5-11)**

Enlarged semi-erect wedge-shaped thorns along midline of trunk and tail present; tail relatively short, length about 1 times disc width ... ***Himantura jenkinsii*** **(p. 5-48)**

Himantura fai Jordan & Seale 1906

Pink whipray

Figures 3.2.1a, 3.2.5a, 3.2.7e, 3.2.8e, 3.2.10v, 3.2.11e, 3.2.12a, 5.2.1–5.2.2;

Tables 5.2.1–5.2.2

Himantura fai Jordan & Seale 1906: 184, fig.2 (original description, figured). Holotype: USNM 51712, 368 mm disc width, female. Type locality: Apia, Samoa (western Pacific Ocean).

Synonymy. —

Trygon purpurea (Smith) Müller & Henle 1841: 160, pl. 52 (original description based on drawing by A. Smith in the British Museum, no designated types). Type locality: probably South Africa.

Trygon liocephalus Klunzinger 1871: 678 (original description based on a foetus from a female of 1 m disc width, not figured). Holotype: ZMB 8083, 320 mm disc width, female. Type locality: Rqeda, Arab.

Dasyatis purpurea: Barnard 1925, 78 (misidentification in part).

Dasyatis purpureus: Wallace 1967, 50, fig. 24 (description, illustration of a 781 mm disc width, young female). Locality: Durban Bay, South Africa.

Dasyatis fluviorum (not Ogilby): Fourmanoir & Laboute 1976, 362 (description, misidentification, figured). Locality: Caledonia.

Himantura granulata (not Macleay): Coleman 1981, 23 (habitat, figured, misidentification). Localities: Queensland; New South Wales in Australia.

Himantura sp.: Compagno 1986, 140, fig. 30.11 (brief description). Locality: Durban Bay.

Himantura sp.: Compagno *et al.* 1989, 106 (brief description, illustrated). Locality: East Coast off Durban Bay, South Africa.

Himantura uarnak (not Forsskål): Lester & Sewell 1989, 103 (misidentification; see Whittington and Last 1994).

Himantura sp. 2: Michael 1993, 88 (brief account, figured).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, centrally robust; preorbital snout short, apical lobe almost indistinct; anterior disc margin broadly convex; lateral apices moderately angular. Orbits moderately large. Dorsal surface of disc uniform grey to light brown, ventrally white with dark grey disc margin, including posteror-lateral corner of nasal curtain gill slits, pelvic fins and ventral of tail base; tail uniformly black. Denticle band along mid-trunk sparse until about 500 mm disc width, mid-scapular denticle inconspicuous, thorns absent. Pelvic girdle almost triangular, puboischiadic bar acute anterior-medially.

Description. — Disc rhomboidal, width 1.12-1.18 times length; robust, centre raised at mid-scapular, maximum disc thickness 9-14% of disc width (DW); preorbital snout short, broadly convex, with an almost indistinct apical lobe, angle 124-129^{O}; anterior margins of disc broadly convex, lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.1-5.2.2). Pelvic fins rather short, 13.4-18.9% DW; width across base 10.2-12.7% DW. Claspers of adult male (Fig. 3.2.5a) long and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle long, about 2/3rd of clasper length on its outer margin, prominent notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.03-2.63 times disc width; base narrow, subcircular in cross-section, width 1.06-1.28 times height at base.

Snout short, depressed; preoral snout length 2.28-2.95 times mouth width, 1.85-2.39 times internarial distance, 18.0-20.1% DW; direct preorbital snout length 1.34-1.83 times interorbital length, horizontal length 1.19-1.81 times interorbital length; snout to maximum disc width 31.8-39.2% DW; interorbital space flat; eye moderately large, diameter 36-61% spiracle length; orbits slightly protruded, diameter 0.75-1.14 in spiracle length, interorbital distance 1.77-2.16 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostril moderately large, laterally expanded, outer margin with a weak double concavity, length 0.44-0.54 in internasal distance; internasal distance 0.55-0.72 of prenasal length, 1.85-2.26 times nostril length. Nasal curtain skirt-shaped, broad, width 1.85-2.37 times length;

lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 4 short, well-developed papillae; medial pair simple, rounded distally, longitudinally flattened, subequal in size and almost three times larger than outer pair, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair.

Teeth small, smaller in upper jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth rows 20-22 in upper jaw, 28-31 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.19-1.67 times length of fifth, 0.34-0.42 of mouth width; distance between first gill slits 1.28-2.10 times internasal distance, 0.31-0.48 of ventral head length; distance between fifth gill slits 1.28-2.07 times internasal distance, 0.29-0.50 in ventral head length.

Squamation. — Stages of squamation with narrow size ranges, with Stages 1 and 2 simultaneously developing. Development of primary denticle band simultaneous with centre of disc appearing raised. Tail only sparsely covered with denticles except in very large adults (> 1m DW).

Holotype in early part of Stages 1 and 2 (Fig. 5.2.1): its dorsal surface mainly smooth, with evidence of a weak primary denticle band above first synarcual, and mid-dorsal region from end of cranium to rear of scapular scattered with numerous fine denticles; without prominent suprascapular denticle. Denticles in primary band narrow heart-shaped, size almost twice as large as those in secondary denticle patch. Tail with small denticles scattered on its dorsal surface, and a row of 10 large spinules pre-sting (Jordan & Seale 1909).

Stage 0: from birth (ca. 300 mm DW) — Disc entirely smooth; without suprascapular denticle.

Stage 1-2: (ca. 360-500 mm DW) (Figs. 5.2.1-5.2.2) — Development of primary, median denticle band above first synarcual simultaneous with initial development of discontinuous secondary denticle patches, defining the early part of this stage. Primary band developing as a single row of uniformly wide-spaced narrow heart-shaped denticles with base entirely embedded in skin.

As the development progresses, more denticles appearing in patches above abdomen and interorbital; patches weakly coalesce through a scattering of widely spaced median connective denticles, forming a rectangular-shaped band with weakly defined margin above mid-scapular region.

Primary denticle band becomes prominent in specimens of around 500 mm DW.

Denticles uniform flat narrow heart-shape to blunt conical, widely spaced with about 1-3 denticles apart; size largest (4 mm) along mid-trunk, gradually decreasing towards band margin.

Stage 4: (>500 mm DW) — In early part of this stage (500–700 mm DW), cranial and scapular denticle patches coalesce to form an irregular longitudinal band, terminating just after scapular, not extended to abdomen. Denticles increasing in number, but remain widely spaced.

Late stage four (>900 mm DW), secondary band well-developed, continuous along trunk and tail; subrectangular, width confined to interspiracular width, slightly constricted around nape and just after scapular, margin well-defined; anteriorly extending to just in front of orbits, ratio of naked area on snout to preorbital snout length 67.3-100.2%; posteriorly narrowing sharply a short distance becoming as wide as tail width at pectoral-fin insertion, before extending weakly onto tail, to sting base. Denticles largest along dorsal surface and near tail base, decreasing towards tail tip, minute along ventral surface of tail; conical denticles present on all surfaces of tail, spinulous denticles present on posterior half between tail base and sting base. Outside of secondary band, skin smooth, void of denticles, except on posterior tip of pectorals, minute granulous denticles present, confined to a narrow margin. Primary denticle band becomes obsolete at this stage.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine.

Meristics. — Total pectoral-fin radials 154 (155-157, n=3); propterygium 61-62 (61-63), mesopterygium 19 (18-21), metapterygium 73-74 (72-76); pelvic-fin radials 25-27 (23-27, n=3); vertebral segments 118 (120-123, n=2), monospondylous 51 (48-52, n=2), prespine diplospondylous 67 (71-102, n=3) and postspine diplospondylous 0 (0, n=3).

Colour. — In fresh, disc uniform light brown to uniform greyish with pinkish margin around entire disc. Disc plain without any reticulation or spotting, except for dark dendritic markings of the sensory pore opening on outer margin of pectoral and on snout; such markings although commonly visible (as illustrated in original description; Jordan & Seale 1906: 184, fig. 2), is sometimes weakly evident. Small white patch in front of orbits and anterior end of spiracle margin. Ventral disc uniform pale with broad dark margin beginning apex of pectorals, continuing to its posterior tip; dark colouration widest at margin of pectoral-fin apex, narrowing to edge along anterior disc margin; narrower dark margin on pelvics, width about half that on pectorals; blotches of dark colouration present on ventral snout; dark streaks also on free rear tip of nasal curtain, and lining of gill slits. Tail uniformly black after short distance from tail base, about midway between tail base and sting base; ventral tail base with a narrow pale area, becoming blackish from about a third between tail base and sting base, wholly black beyond to tail tip; laterally with irregular blackish margin continuing from dorsal surface, to a short distance from tail base.

Figure 5.2.1. Holotype of *Himantura fai* in dorsal and ventral views. a, dorsal disc (disc edge curled); b, ventral disc; c, close-up of scapular denticles; d, close-up of oronasal (nasal curtain distorted); e, pelvic-fins and cloacal region. USNM 51712 (368 mm DW; female; Apia, Samoa). Photos by S. Raredon. Bars 10 cm.

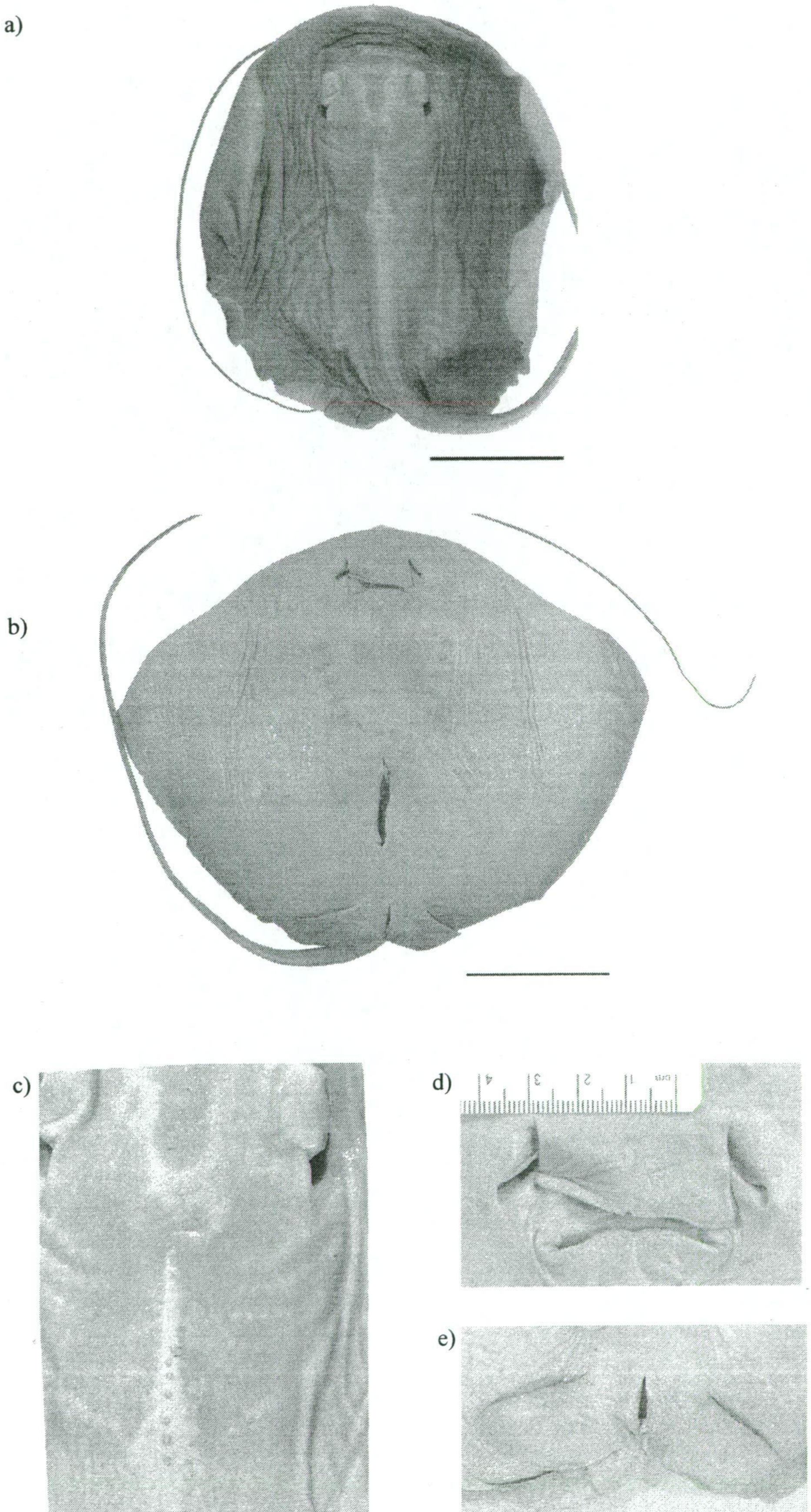
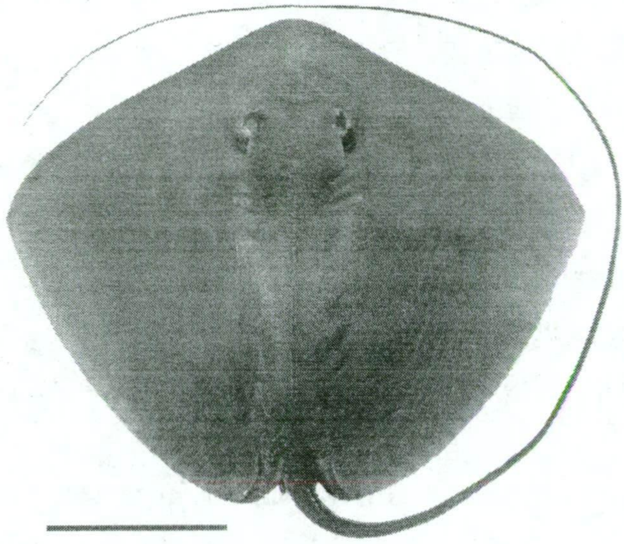
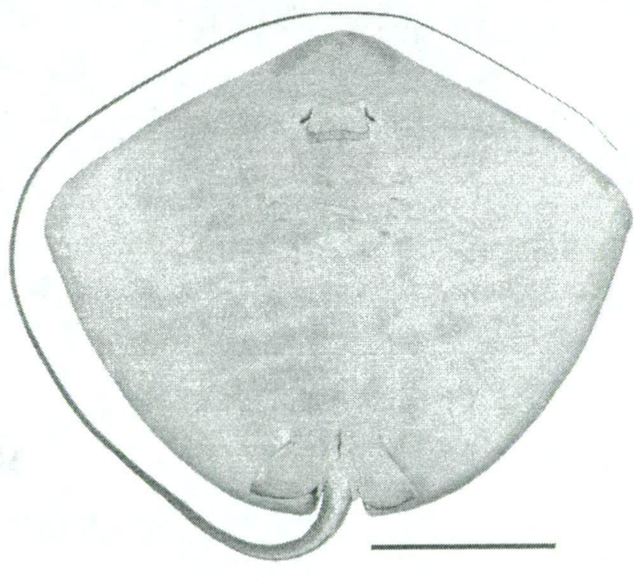

a)
b)
c)
d)
e)

Figure 5.2.2. Representative specimen of *Himantura fai* in dorsal and ventral views. a, dorsal disc (note sparse denticle band); b, ventral disc; c, close-up of oronasal. CSIRO H5207.01 (557 mm DW; immature male; Gulf of Carpentaria, Australia). Photos by T. Carter. Bars 10 cm.

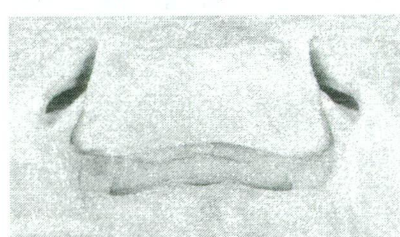
a)



b)



c)



Skeletal morphology. — Neurocranium of 309 mm DW immature male (Figs. 3.2.7e, 3.2.8e) with moderately elongate nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval; distinctive keyhole-shaped anteroposterior fontanelle, which extends to level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, just anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes elongate and robust, rod-like throughout, posteriorly rounded; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with straight margins; lateral commisure broad.

Scapulocoracoid of 650 mm DW immature male (Fig. 3.2.10v) relatively narrow, high, posterior part strongly extended in lateral view; lateral face subtriangular, with broad base tapering sharply upwards and medially to narrow articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra, not visible in lateral view. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5-3 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle of 650 mm DW immature male (Fig. 3.2.11e) narrowly arched, relatively thick, median prepelvic process present, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium of 1080 mm DW mature male (Fig. 3.2.12a) relatively simple; structure of basal segments unknown (clasper specimen was cut halfway along the axial); beta cartilage present as a separate element, merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, spoon-shaped, posterior edge merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, oval subrectangular, and scoop-shaped; terminal tip of axial cartilage short, spatula-like; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, and narrowly extending to lateral surfaces.

Size. — Birth size around 300 mm DW; length at first maturity (males) between 800 and 900 mm DW. Males with 560 and 650 mm DW from the Gulf of Carpentaria (Australia), and Sandakan (Sabah, Malaysia) respectively, are both immature (maturity stage 1-2), while another male specimen from Indonesia (CSIRO H4426.33; only clasper saved) 1080 mm DW, as mature (maturity stage 4). Females reaching to around 1000 mm DW, as based on a specimen (MTUF 26717) from Micronesia.

Etymology. — Not specified, but probably after its common name in local dialect.

Common names. — 'Fai' (Jordan & Seale 1906); Pink whipray (Last & Stevens 1994).

Distribution. — Widely distributed in the South China Sea and Indian Ocean, although most reports mention this species as uncommon. Across the Indo-West Pacific, positive records are reported from South Africa (Last & Compagno 1999), Suez, Egypt (R. Bonfil pers. comm.), Andaman Sea (Kuiter & Debelius 1994), Ryukyu Islands (Yoshigou & Yoshino 1999), South China Sea and Sulu Sea off Sabah (Fowler *et al.* 1999; this study), northern tropical Australia including the Java Sea, down to New South Wales (Last & Stevens 1994; Whittington & Last 1994), Caroline Islands (Homma *et al.* 1994), Orangere Bay, Papua New Guinea (P. Kailola pers. comm.), Eiao, Marquesas Islands (J. Randall pers. comm.), and Apia, Samoa (Jordan & Seale 1906).

This species appear to prefer soft sandy bottom to one of coral rubble; capture depths to between 27–68 m. Commonly present in aggregations of two or more individuals, they are observed to partially lay on top of one another.

Comparisons. — *Himantura fai* is closest to *H. jenkinsii* Annandale, both being similar in overall disc shape, although distinct from the latter by absence of enlarged thorns along the trunk, as well as dissimilar in several neurocranial features. In *H. fai,* the antorbital condyle is located on the anterolateral edge of the nasal capsule below the preorbital process, and in *H. jenkinsii*, this structure is located on the anterolateral surface between the edge of the nasal capsule and the preorbital process. The postorbital processes of *H. fai* are rather anteriorly directed, compared to *H. jenkinsii* which are more laterally directed.

Remarks. — Jordan and Seale (1906) noted this species as allied to *H. uarnak*, but did not state the reason. Several reviewers, namely Garman (1913) and Fowler (1941), later erroneously synonymized this species with another species, most likely due to the similarity in overall disc shape, but this is not clear from the texts.

No measurements on the holotype were made as the specimen was not available for loan, and it was not possible to personally visit the museum. Nevertheless, staff at the USNM were helpful in providing digital colour images and x-radiographs of the specimen, from which limited external morphological observations and meristic counts were obtained. The tooth counts given by Jordan and Seale for the upper jaw seem unusually low, but this is likely due to different counting method. Unfortunately, they did not specify their method used. The 7 enlarged denticles above the synarcual, referred to as 'spines' by Jordan and Seale, are really narrow heart-shaped denticles with dorso-posteriorly pointed tip.

The birth size given as 'about 55 cm disc width, 154 cm total length' by Last and Stevens (1994) is erroneous, as the size of the holotype is much smaller at 370 mm DW, and appear as if it had been born for sometime before being discovered as based on its colour images. On the other hand, one of the smaller specimen examined (CAS 213286 [3 of 3], 320 mm DW) still had an intact umbilical cord, as with the holotype of *Trygon liocephalus* Klunzinger which has the same disc width size (Klunzinger 1871). It is noted that the latter (holotype of *T. liocephalus*) was also not personally examined, and that the observations made were based on colour photographs.

The nominal species *Himantura purpurea* (Smith) Müller and Henle 1841, as resurrected by Wallace (1967) based on specimens recorded from off South Africa, indicated the specimens he used in his description (which included an illustration and several measurements), is actually *H. fai* Jordan and Seale. Since Wallace did not mention *H. fai* in his comparison, this suggests he might have not been aware of Jordan and Seale's paper (describing *H. fai*). On the other hand, Barnard (1925) appear to have erroneously misidentified *Dasyatis (Pteroplatytrygon) violacea* as *H. purpurea* based on the 'broadly convex snout', and dark purplish colour of the species as described by Müller and Henle. The name *H. purpurea* is considered as a senior synonym because of the lower frequency of its usage compared to *H. fai*, i.e. it had been in use for less than 10 times (minimum frequency usage to be recognized is 25 times) in the immediately preceding 50 years (Article 23.0.1.2, ICZN 1999). Compagno and Heemstra (1984) were also convinced that reports of *Himantura* sp. from South Africa as rather possibly *H. fai*.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CAS 213286(3of3), CAS 213290 (Thailand); CSIRO H687.2, CSIRO H1910.1, CSIRO H5671.01 (NW Shelf, WA, Australia); CSIRO H1489.2 (NW of Dampier Archipelago, WA); CSIRO H2753.01, CSIRO H2754.01, CSIRO H2756.01 (Heron Island, QLD, Australia); CSIRO H3355.01, CSIRO H3378.01, CSIRO H5207.01[a,e] (G of Carpentaria, QLD, Australia); CSIRO H4426.33[b] (Java, Indonesia); CSIRO H5480.01[b,e] (Sandakan, Sabah, Malaysia); MTUF 26717 (Micronesia); USNM 51712[c,d] (holotype) (Apia, Samoa).

Himantura gerrardi (Gray 1851)

White-spotted whipray

Figures 3.2.2a, 3.2.5b-c, 3.2.6g-h, 3.2.7f, 3.2.8f, 3.2.10b, 3.2.11f, 5.2.3–5.2.8; Tables 5.2.3–5.2.4

Trygon gerrardi Gray 1851: 116 (original description based on 2 stuffed specimens from Mr. Argent's collection, one of them given as 8.25 inches disc width, approximately 209 mm disc width, not figured). Syntypes: ?BMNH 1843.5.19.1, 148 mm disc width; ?BMNH 1846.11.18.49, 218 mm disc width. Type locality: Indian Ocean near India.

Synonymy. —

Trygon macrurus Bleeker 1852: 74 (original description based on 6 specimens, 3 males, 180-295 mm disc width, not figured). Possible syntypes: NMV A949, 252 mm disc width, female; BMNH 1867.11.28.160, 194 mm disc width (measurement by P. Last), immature male; RMNH 2460, 254 mm disc width (measurement by P. Last), female (dried and stuffed); RMNH 2468, 290 mm disc width (measurement by P. Last), female (dried and stuffed); RMNH 2469, 197 mm disc width (measurement by P. Last), female (dried and stuffed). Type localities: Batavia (=Java), Samarang (=Semarang), and Padang (all three localities in Indonesia).

Trygon (Himantura) gerrardi: Günther 1870, 474 (brief description). Localities: East Indian archipelago and Japan.

Leiobatis (Himantura) gerrardi: Bleeker 1877, fig. 1, pl. 559, Plagiostom. Pl. 37 (illustration of unidentified male syntype).

Trygon alcockii Annandale 1909: 27, fig. 3 (original description based on two specimens, one saved as the holotype; illustrated). Holotype: F 2474/1 in the Indian museum, disc width not stated, mature female. Type locality: Puri, Orissa coast, India on 21st March 1909.

Dasybatus (Himanturus) gerrardi: Garman 1913, 377 (brief description, misidentification in part). Localities: India; East Indies.

Dasyatis gerrardi: Fowler 1928, 16 (brief description, misidentification in part). Localities: Zanzibar to the East Indies.

Dasyatis uarnak (not Forsskål): Fowler 1930, 177 (brief description, illustrated, misidentification in part). Localities: China; East Indies; Philippines.

Dasyatis (Himantura) gerrardi: Fowler 1941, 409 (description after Gray).

Trygon uarnak (not Forsskål): Anon. 1955, 9 (description, misidentification). Locality: Pakistan.

Himantura gerrardi: Compagno & Roberts 1982, 323 (listed, distribution limits).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, trunk moderately raised. Dorsal surface with white spots or specks, scattered on entire dorsal surface or confined to posterior half of disc, spots extending onto lateral and dorsolateral surface of tail base until sting base; distance between spots more than diameter of largest spot apart. Tail banded beyond sting in both young and adults; banding usually more readily visible compared with white spots on disc. Primary denticle band absent. Secondary denticle band subrectangular, with well-defined margin; band extending along trunk from preorbital to tail base, its width confined to interspiracular distance; fully developed by 314 mm disc width.

Description. — Disc rhomboidal, width 1.06-1.19 times length; mid-scapular moderately raised, maximum disc thickness 9-14% of disc width (DW); preorbital snout moderately long, pointed apical lobe relatively narrow and distinct, angle 108.5-124^{o}; anterior margins of disc slightly concave, lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.2.6). Pelvic fins short, 16.3-21.6% DW; width across base 9.6-13.8% DW. Claspers of adult male (Figs. 3.2.5b,c) long and stout, dorsal surface slightly convex, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; large ventral terminal cartilage, its length about half length of the clasper from pelvic-fin insertion; lining of pseudopera smooth; hypopyle short, about 1/3rd of clasper length on its outer margin, without prominent anterior notch. Tail slender and whip-like, tapering gently toward sting and tail tip, length 2.70-3.40 times disc width; base slightly depressed in cross-section, width 0.85-1.79 times height at base.

Snout moderately long, depressed; preoral snout length 2.80-3.53 times mouth width, 2.32-2.99 times internarial distance, 19.4-23.2% DW; direct preorbital snout length 1.44-2.17 times interorbital length, horizontal length 1.26-2.03 times interorbital length; snout to maximum disc width 33.4-43.2% DW; interorbital space flat; eye moderately large, diameter 45-96% spiracle length; orbits slightly protruded, diameter 0.76-1.55 in spiracle length, interorbital distance 1.28-2.70 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostril moderately-large, slit-like, laterally expanded, outer margin with a weak double concavity, length 0.36-0.61 in internasal distance; internasal distance 0.44-0.59 of prenasal length, 1.64-2.75 times nostril length. Nasal curtain skirt-shaped, relatively narrow, width 1.54-2.03 times length; lateral margin almost straight, weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave to weakly double concave.

Mouth arched; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2-5 short, well-developed papillae; medial pair variably structured (i.e. either rounded, truncated, bifurcated, or trifucated distally), longitudinally flattened, subequal in size and almost three times larger than outer pair, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair; outer pair small, or absent; fifth papillae sometimes present, located between medial pair.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak. Tooth rows 22-26 in upper jaw, 25-30 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.01-1.79 times length of fifth, 0.28-0.44 of mouth width; distance between first gill slits 1.87-2.53 times internasal distance, 0.38-0.46 of ventral head length; distance between fifth gill slits 1.11-1.63 times internasal distance, 0.23-0.31 in ventral head length.

Squamation. — Stages of squamation with broadly overlapping size ranges; rate of denticle band development higher in juveniles, and faster in males. Development of primary denticle band simultaneous with centre of disc appearing slightly raised (although the trend of disc thickness to disc width ratio indicates a decrease with increase in disc width). Tail entirely covered with denticles especially in adults.

Stage 0: from birth (ca. 180 mm DW) (Figs. 5.2.3-5.2.5) — Disc entirely smooth. Suprascapular denticle(s) appearing during mid-stage; initially weakly evident and entirely covered with skin, soft when first exposed, numbering between 1-4 denticles (usually 2-3); becoming hardened with age, increasing in size (length of largest denticles ranging between 1–4 mm), and more pronounced in shape (seed-shaped to narrow heart-shaped); pale in colour, variable whitish to yellowish.

Stage 1: (ca. 200-260 mm DW) — Development of primary denticle band around nuchal region. Band developing as a narrow series (1-3 rows) consisting of small and large denticles (usually smaller than suprascapular denticles); those in median row larger than on adjacent outer. Denticles flat heart-shape, closely set, not imbricated.

Stage 2: (ca. 250-300 mm DW) (Figs. 5.2.6-5.2.7a,b) — Initial stage for development of discontinuous secondary denticle patches; onset around primary band, forming scapular patch, followed by development of cranial patch. Denticles with flat crowns, varying from ovate to heart-shape, closely set; size smaller than suprascapular and primary denticles. Primary denticle band becomes obsolete at this stage.

Stage 4: (ca. 280 mm DW) (Figs. 5.2.7c,d,e-5.2.8b,c) — In early part of this stage, cranial and scapular denticle patches coalesce to form a regular longitudinal band, terminating at tail base. Denticles remain dense and closely set.

Late stage four, secondary band well-developed, continuous along trunk and tail; subrectangular, width confined to interspiracular width, margin well-defined; anteriorly extending well forward of orbits, ratio of naked area on snout to preorbital snout length 64%; slightly expanded above abdominal region, diverging anteriorly for a distance equivalent to a spiracle length at pectoral-fin insertion; extending on to tail, across almost entire surface of dorsal half, lateral and ventral surfaces of tail naked. Denticles largest along median dorsal, including interorbital, decreasing towards margin. Outside of secondary band, skin smooth, void of denticles.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine, second sting rarely present.

Meristics. — Total pectoral-fin radials 129-140 (n=49); propterygium 48-53, mesopterygium 19-24, metapterygium 58-67; pelvic-fin radials 22-31 (n=49); vertebral segments 106-118 (n=43), monospondylous 41-56 (n=49), prespine diplospondylous 58-73 (n=43) and postspine diplospondylous 0 (n=39).

Colour. — In fresh, disc olive green to greenish grey dorsally (becoming darker in preservative), usually with diffuse pattern of white spots or specks (spots in adults often faded); spots if present, usually visible in preservative; posterior edges of disc paler and pinkish; tail banded beyond sting in both young and adults, banding pattern more readily visible than white spots in preserved materials. Ventral surface of disc and pelvic fins usually uniformly white, sometimes with narrow band of light-brown on posterior disc margins. White spots generally distributed over entire disc surface, often confined to posterior surface around tail base, or entirely absent. Two spots occasionally coalesced, especially on posterior disc of mature adults. More rarely, white crescentic patterns present on posterior disc of mature adults, continuing on to tail base (observed in two large females - Figs. 5.2.7d,e). Alternating dark-brownish and whitish tail bands uniformly wide, except around mid-length of tail and near tail tip; within these segments, 2-3 bands narrower than the rest usually present.

Skeletal morphology. — Neurocranium of 750 mm DW female (Figs. 3.2.7f, 3.2.8f) with moderately elongate nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval, internasal moderately broad; fontanelle triangular-shaped anteroposteriorly, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen just below optic stalk on lateral surface of basal plate, midlength of cranium; preorbital processes moderately elongate, basally triangular and posteriorly rounded; supraorbital crests low, slightly concave along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commisure broad.

Scapulocoracoid (Fig. 3.2.10b) relatively broad, low, posterior part strongly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a large postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11f) broadly arched, relatively thick, median prepelvic process absent, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

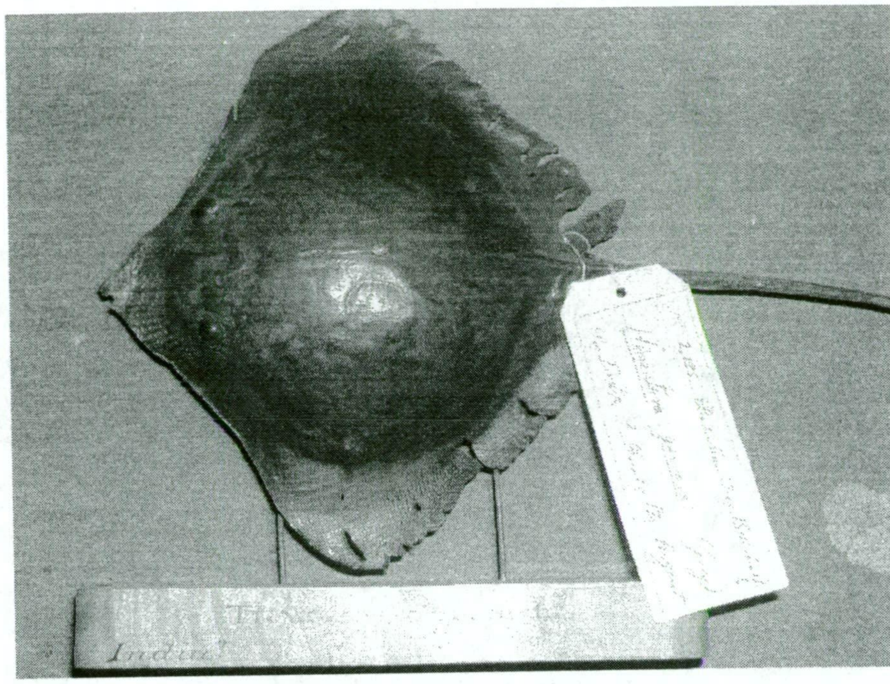
Mixopterygium of adult males unknown.

Size. — Birth size around 180 mm DW; length at first maturity (males) between 450 and 550 mm DW. A 396 mm DW male specimen (CSIRO H4927.05) was determined as being an adolescent (maturity stage 3), while another male specimen (CSIRO H4918.02) 532 mm DW, as almost mature (early maturity stage 4). As for females, two late-term gravid specimens were observed at 540 and 550 mm DW (newborns saved as CSIRO H5480.04 and CSIRO H5474.04 respectively); specimens of up to 630 mm DW have been observed from fish markets in Malaysia.

Etymology. — Not specified, but probably after a person called '*Gerrard*'.

Figure 5.2.3. One of two syntypes of *Himantura gerrardi* in dorsal views. a, close-up of disc, indicating midscapular denticles; b, whole specimen, including tail (note banded tail). BMNH 1843.5.19.1 (India). Photos by P. Last.

a)



b)

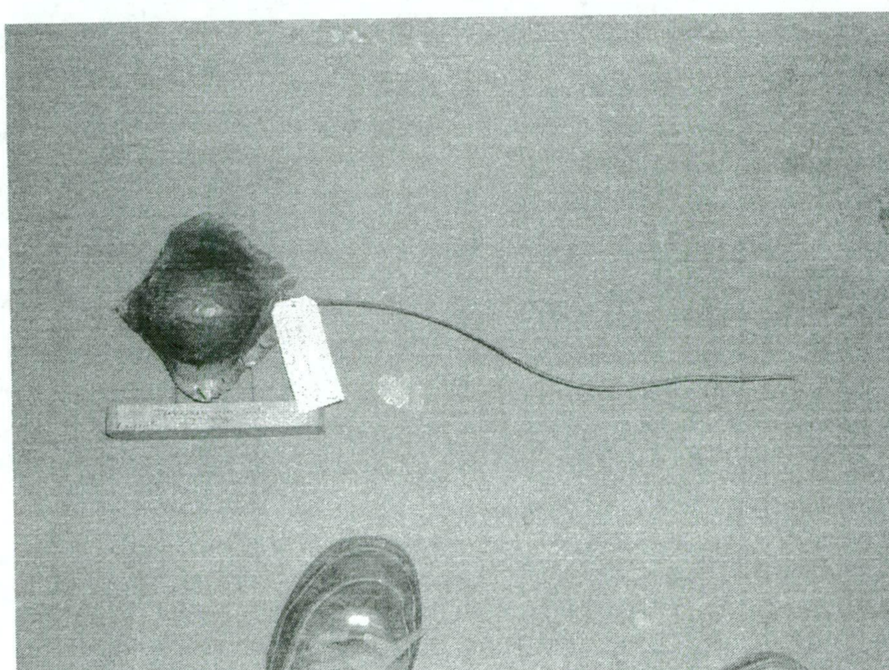
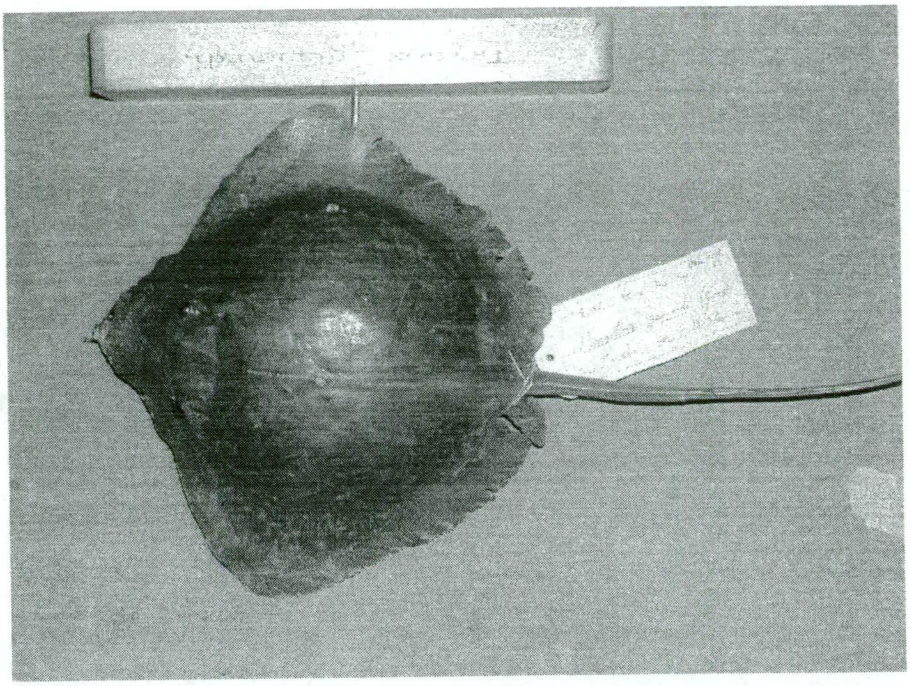


Figure 5.2.4. One of two syntypes of *Himantura gerrardi* in dorsal views. a, close-up of disc, indicating midscapular denticles; b, whole specimen, including tail. BMNH 1846.11.18.49 (India). Photos by P. Last.

a)



b)

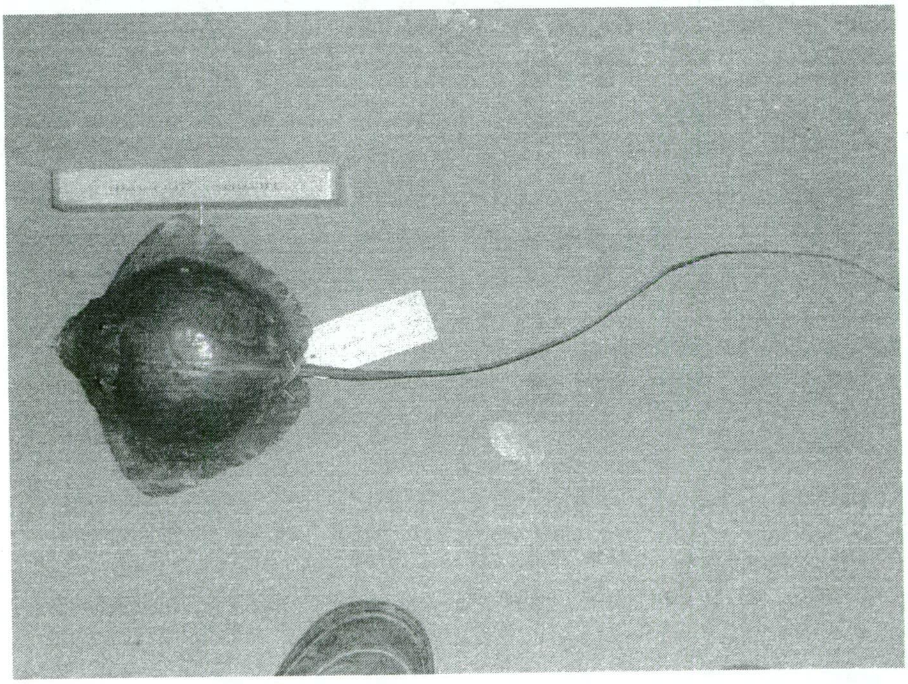


Figure 5.2.5. Illustration of *Himantura gerrardi* (reproduced from Bleeker 1877: fig. 1, pl. 559, Plagiostom. Pl. 37).

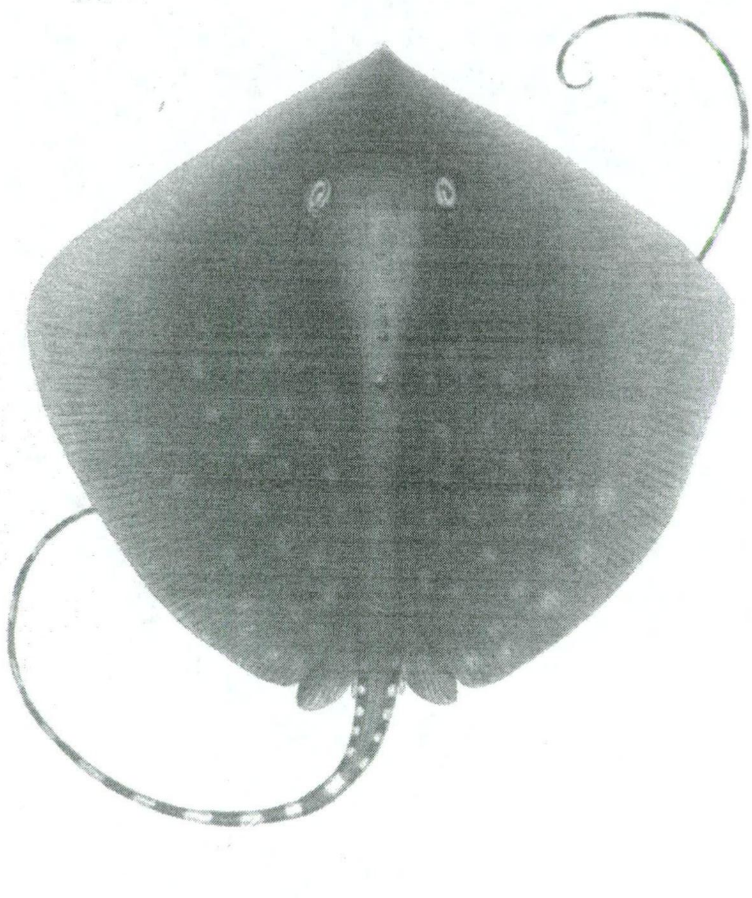


Fig. 1 Leiobatis (Himantura) Gerrardi Blkr.

Figure 5.2.6. Representative specimens of *Himantura gerrardi* var. 'small denticle' in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of oronasal; d, oronasal (nasal curtain folded back). CSIRO H5476.01 (301 mm DW; female; Kota Kinabalu, Sabah, Malaysia). Bars 10 cm (a-b), 10 mm (c-d). Note: a & b taken when fresh and mouth not slit.

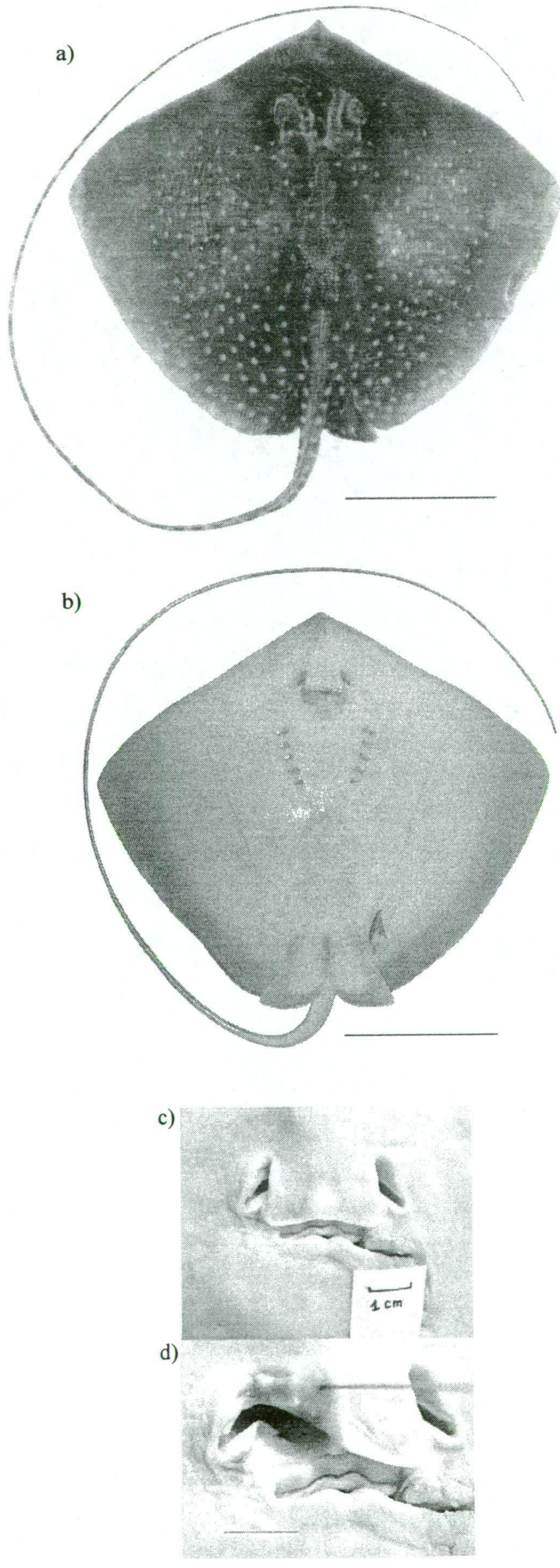

a)
b)
c)
1 cm
d)

Figure 5.2.7. Representative specimens of *Himantura gerrardi* var. 'small denticle' indicating squamation and intraspecific colour variation. a, 256 mm DW (CSIRO H5476.07; female; Kota Kinabalu, Sabah, Malaysia; photo by T. Carter); b, 276 mm DW (CSIRO H4426.24; immature male; Muara Angke, Jakarta, Indonesia; photo by T. Carter); c, 381 mm DW (SMKK SKN22-4496; female; Sandakan, Sabah, Malaysia; photo by G. Yearsley); d, 470 mm DW (UMS MMSK36; female; Sandakan, Sabah, Malaysia); e, 550 mm DW (UMS MMKK24; female with end-term pup; Kota Kinabalu, Sabah, Malaysia). Bars 10 cm.

a) b) c) d) e)

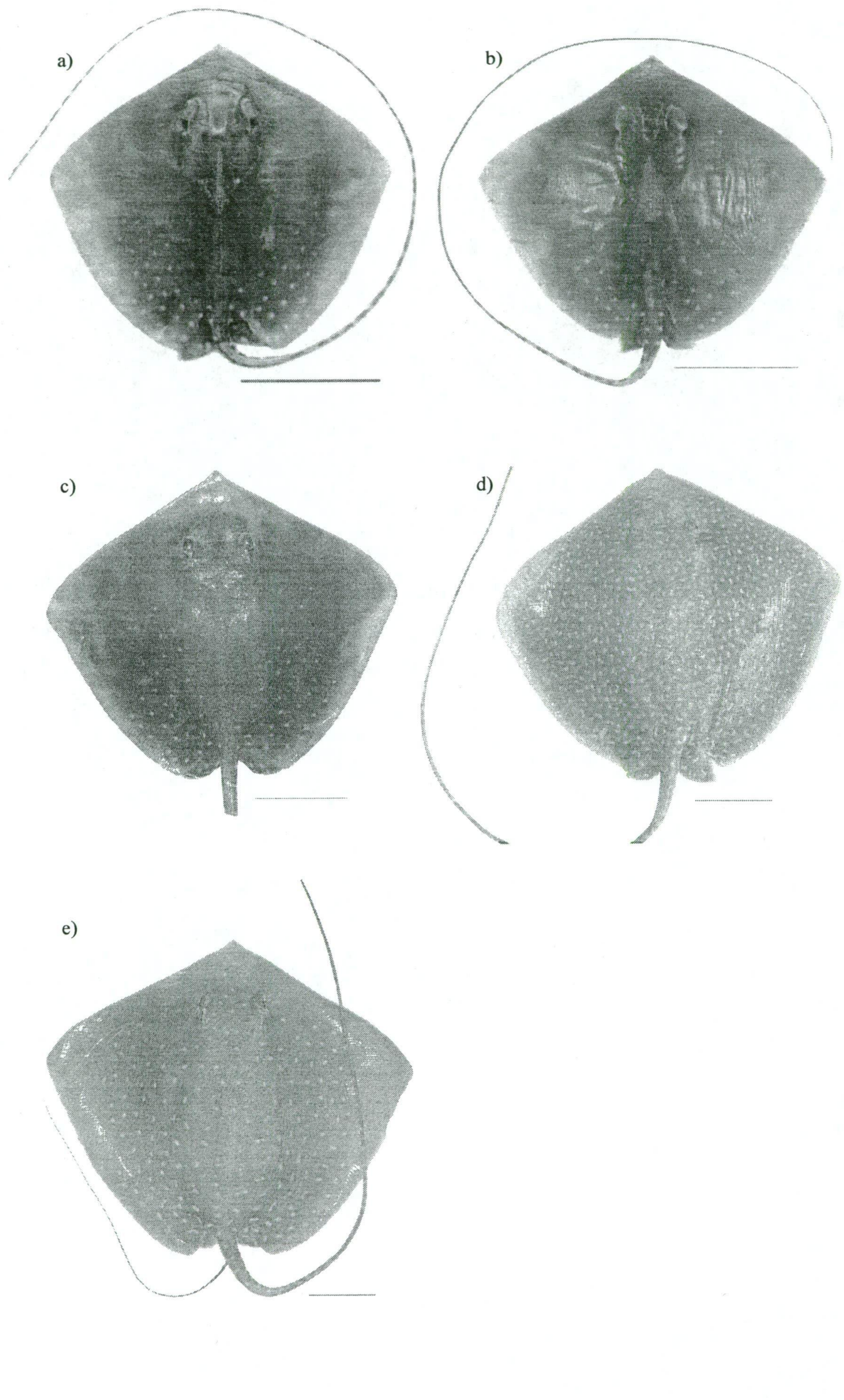
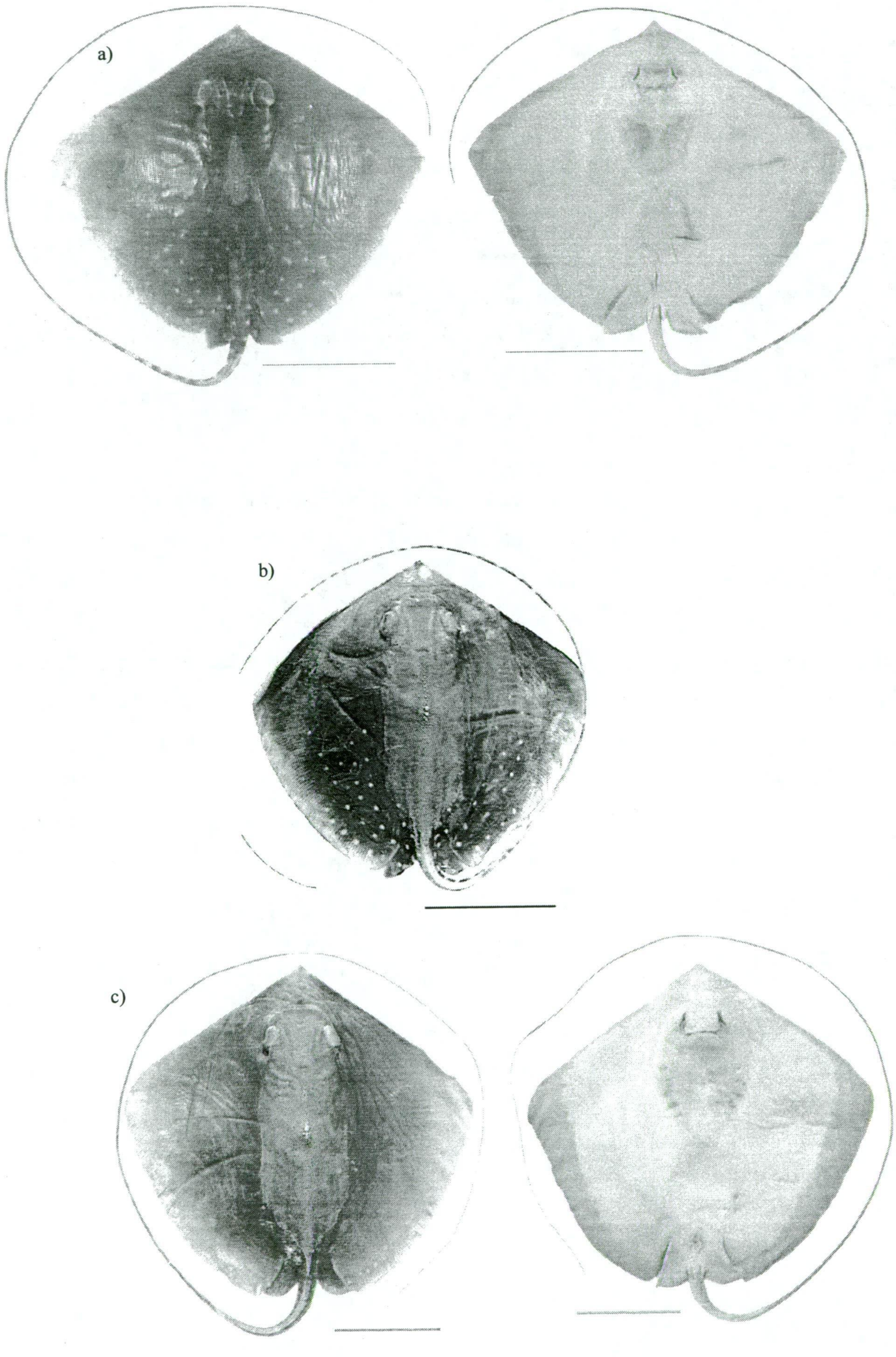


Figure 5.2.8. Representative specimens of 'small denticle' and 'large denticle' var. of *Himantura gerrardi* (note intraspecific colour variation, size of the midscapular denticles, and disc width, i.e. wider in 'small denticle' var.). a, var. 'small denticle' (277 mm DW; CSIRO H4426.24; immature male; Muara Angke, Jakarta, Indonesia); b, var. 'large denticle' (277 mm DW; CSIRO H5479.05; immature male; Sandakan, Sabah, Malaysia); c, var. 'large denticle' (316 mm DW; CSIRO H5484.04; immature male; Semporna, Sabah, Malaysia). a, c: photos by T. Carter. Bars 10 cm.


a)
b)
c)

Common name. — White-spotted whipray.

Distribution. — Widely distributed throughout the inshore Indian Ocean, South and East China Seas (e.g. Annandale 1909, 1910; Shen 1993; Last & Compagno 1999). Reports of the species is often confused with *H. uarnak* (e.g. Chaudhuri 1911; Devanesen & Chidambaram 1953; Mohsin & Ambak 1996), but records from Samoa (Fowler 1956), Pakistan (Bianchi 1985), Sri Lanka (De Bruin *et al.* 1995; Morón *et al.* 1998) are probably correct. Records from elsewhere in the Indo-Pacific (e.g. Compagno 1986; Compagno *et al.* 1989) may represent a separate species, identified as *H.* sp. B in this study (see Comparisons).

Comparisons. — The specimens examined exhibit variation in supra- or mid-scapular denticle size, tentatively termed the 'large denticle' variety, as opposed to the 'small denticle' variety (Fig. 5.2.8). The large denticle variety tend to have darker disc, the tail only dorsally banded, and less pronounced banding in both young and adults. Separate analyses of the datasets indicate the proportional measurements and meristics of both morphs overlap (Tabs. 5.2.2b, 5.2.4b). It is noted however, that because all specimens of the 'large denticle' variety were obtained from the eastern coastal markets of Sabah, there are a possibility this variety may be representing specimens of different populations, or even of different species from the 'small denticle' variety. More specimens, representing both forms are required to ascertain their status.

Three other very similar species identified during the course of this study exists, and are tentatively named as *H.* sp. B (Arabian banded tail), *H.* sp. C (Pakistan whipray) and *H.* sp. D (short-tail whipray). *Himantura gerrardi* is distinguished from these three species by a combination of characters, i.e. disc slightly wider than long, squamation (including shape of suprascapular denticles, shape and size of denticles in band, and rate of squamation), and colouration of dorsal disc, including pattern of tail banding.

Remarks. — Specimens obtained and/or observed in the field, and tentatively identified as *H. gerrardi*, include a number of colour variations, but all with banded or patterned tails (Figs. 5.2.6-5.2.8). Annandale (1909) probably started the trend of using the white spots on the disc as a diagnostic characteristic for *H. gerrardi*. In the same report, he described *Trygon alcockii* based on a mature female specimen from Puri, India. In comparing this species with *T. gerrardi* (=*H. gerrardi*), Annandale noted differences in disc proportions, and in the distribution of white spots on the disc, i.e. scattered on the entire dorsal surface of the disc in the new species. However, Annandale's description on *H. gerrardi* appears to contain misidentifications in his description of the appearance of cream-coloured spots with age of the stingray. Thus, due to the overlapping colour variations observed in both large and small denticle varieties during the present study, further discussed below, *T. alcockii* is herein treated as a junior synonym of *H. gerrardi*.

Trygon gerrardi was briefly described by Gray based on two stuffed specimens in the collection of the British Museum, in his effort to list fish species in the museum. Several direct distance measurements were given (unit in inches), but it is not clear from his paper whether this was based on a single specimen, or otherwise (i.e. the average measurement of the two). Details (i.e. registration numbers) of the specimens were also not provided. Nevertheless, based on the description of squamation, and measurements given, it is obvious that the species description was based on small, juvenile specimens.

Another nominal species, *Trygon macrurus* described by Bleeker in 1852, is often placed in the synonymy of *Himantura gerrardi* (e.g. Compagno & Roberts 1982). However, it is perhaps by common assumption that Bleeker himself may have actually synonymized *T. macrurus* with *H. gerrardi*, when in a much later publication, a colour illustration of what appeared to have been described as the former was labeled as '*Leiobatis (Himantura) gerrardi* Blkr.' (Bleeker 1877: pl. 558 [Plagiostom. Pl. 37], fig. 1). The figure, as with all the other stingray illustrations in his ichthyological atlas, does not provide any explanatory text, or even a scale or size.

The figure of *Leiobatis (Himantura) gerrardi* Blkr. appears to somewhat fit Bleeker's description of the male specimen of *T. macrurus*, and in particular, the following segment as copied from the original text, '...back completely smooth or median line with only a single tubercle; tail more than three times as long as disc, completely smooth except for the large spine, no vestige of fin; genital appendages shorter than ventral fins, conical, posteriorly sulcate, not valvate; body brownish green above, unspotted or with round, yellowish spots; whitish beneath; tail with brown and yellow rings' (as translated from the Dutch and Latin text by P. Aukland).

The description of *T. macrurus* was based on six specimens, of equal number of males and females, ranging between 180 mm DW to 296 mm DW, where Bleeker (1852) gave the type localities as Batavia (=Jakarta), Samarang and Padang, all of which are in Indonesia. In the 'Notes' section of the description, Bleeker mentioned, '...the largest of my specimens, a female, has a completely smooth back, as have two smaller males...' (translation by P. Aukland). This is supposedly the one measuring 295 mm DW. Therefore, the illustrated male specimen cannot be bigger than 295 mm DW.

What appears as more striking though, is the squamation depicted in Bleeker's 1877 figure, and as described above, seem exactly as that described Gray (1851), '...upper surface quite smooth, with the exception of three very small, and one larger, oblong, osseous (bony), tubercles, in the center of the dorsal line; tail smooth'. However, with respect to the colour of the disc, it is more like that described by Bleeker (1852) for *T. macrurus*. Gray described the colour of *H. gerrardi* as '...uniform pale brown with about sixty-five distinct white rings upon the tail...'. It is possible that Gray's specimens were indeed 'plain', or that the spots may have become faded in the stuffed (curated) specimens. Bleeker's illustration of *H. gerrardi* is here reproduced (Fig. 5.2.5) in grayscale.

Eschmeyer (2001) listed three specimens as possible syntypes of *T. gerrardi* Gray, i.e. two of which are stuffed and dried, BMNH 1843.5.19.1 (Fig. 5.2.3) and BMNH 1846.11.18.49 (Fig. 5.2.4), and the third, an alcohol-preserved specimen, RMNH

7442(3). He also listed at least six specimens as possible syntypes and/or Bleeker specimens for *T. macrurus*, i.e. BMNH 1867.11.28.160 (1), RMNH 7442 (1 or more of 3), 8008 (2), 8009 (1 or more of 5), NMV A949 (1), and SMNS 10594 (1).

Of those listed above, eight, in addition to five other non-type specimens in the collection of both museums, were examined in this study. From the results of the examinations, albeit based on photographic images only, it appears most likely that two of the stuffed BMNH specimens designated as possible syntypes for *T. gerrardi*, both fit Gray's description of the species, and seemed to best match that figured by Bleeker (1877: fig.1, pl.37). The matching characters include the general disc shape, but more specifically, the four mid-disc denticles, and banding of the tail. The dorsal discs appear plain, without any observable white spots. Furthermore, the locality of both specimens are stated as India. However, it is not possible to tell whether the sting is present or intact for both specimens from the available colour photographs.

Thus, one possible scenario is that Bleeker (1877) may have based his illustration of *Leiobatis (Himantura) gerrardi* on either one or both of Gray's specimens, which he recognized as the types. However, as mentioned earlier, the dorsal disc patterning (white spots) present on Bleeker's illustration was not mentioned by Gray, because the colour is usually lost in dried specimens. It is possible that Bleeker may have added this, based on his findings on specimens he earlier (1852) described as *T. macrurus*, that 'yellowish spots' on the dorsal surface of the disc were either present or absent. Furthermore, as explicitly stated by Bleeker (1852), the disc is smooth in the largest specimen (295 mm DW) of *T. macrurus* as with two smaller male specimens, thus implying that the other 3 are not smooth. However, if this was so, that the other smaller specimens may have some denticles developing on the dorsal surface, Bleeker did not describe these.

None of the other possible syntypes (Eschmeyer 2001), in particular BMNH 1867.11.28.160, RMNH 7442 (1 of 3) and NMV A949, were devoid of dorsal denticles, but instead all have varying degrees of squamation. The BMNH specimen is a stuffed material of an immature male, 194 mm DW (measured in April 2001 by

P. Last) and its locality stated as from India. Although it is within the given size range (even after taking account of 'shrinkage factor'), and that it is a male specimen which could be one of the two males implied as not having a smooth disc, it being Bleeker's syntype for *T. macrurus* is questionable because of its locality.

As for the RMNH specimens, the information available during this study is limited to several morphometric measurements and a photograph of only one of the three in the series. Apparently, all three are labeled as from 'East Indies' (name formerly applied to southeastern Asia, embracing the Indian subcontinent), and the size of these specimens are approximately 189, 194 and 275 mm DW (measured pre-Last & Stevens 1994 by P. Last). The largest specimen is an immature male preserved in alcohol (photographed), while the condition including sex of the other two is unknown. It (the largest specimen, herein designated to as RMNH 7442[1]) is plain brown, with weak indication of tail banding. Noting that Bleeker's largest female specimen (of *T. macrurus*) is smooth at 295 mm DW, this largest specimen has a well-developed denticle band along the trunk. Thus, the possibility of it as being a syntype of *T. macrurus* is questionable. However, it may possibly still be one of Bleeker's non-type specimens, and are herein considered as conspecific to *H. gerrardi*.

The NMV specimen is an immature female judging from its size, i.e. 252 mm DW, and squamation. The dorsal surface is 'faded' brown, nevertheless there is evidence of faint banding on the tail. A single, small seed-shape mid-scapular present, although a larger one may have been present as well (scar visible), but may have fallen out during preservation or specimen handling. Anterior to it is a row of smaller similarly shaped denticles, forming the early development of the secondary denticle band. Other surfaces of the disc including the tail, smooth. An intact and unbroken sting is present on the tail, although the tail itself is broken at the tip. 'Cracks' on the dorsal surface of the disc, especially around the scapular region, and broken bits on the edges of the disc, indicate that the specimen appear to have been preserved as dry at one stage, but now in ethanol. It is possible this specimen is one of Bleeker's syntypes, based on its size and locality from Indonesia.

Comments on the type status of other specimens listed by Eschmeyer (2001) is not possible as these were not examined during this study.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

Himantura gerrardi: var 'small denticle' — BMNH 1843.5.19.1[c](syntype of *T. gerrardi*), BMNH 1846.11.18.49[c](syntype of *T. gerrardi*) (India); BMNH 1867.11.28.160[c](possible syntype of *T. macrurus*) ('East Indies Archipelago'); CSIRO H4919.01, CSIRO H4919.03, CSIRO H5479.04, CSIRO H5479.09, CSIRO H5479.10, SMKK SKN22-4496, UMS MMSK35[e], UMS MMSK36[e], UMS MMSK37[e], UMS MMSK38, UMS MMSK(c7)[e,?], UMS MMSK(c8)[e,?] (Sandakan, Sabah, Malaysia); CSIRO H4122.01, CSIRO H4122.02, CSIRO H4123.01 (off Beruwala, Sri Lanka); CSIRO H4426.20, CSIRO H4426.21, CSIRO H4426.22, CSIRO H4426.23, CSIRO H4426.24 (Java, Indonesia); CSIRO H4922.01, CSIRO H4922.02, CSIRO H4922.03, CSIRO H5284.01, CSIRO H5284.02, CSIRO H5284.03[a], CSIRO H5284.04[b], CSIRO H5474.03, CSIRO H5474.04, CSIRO H5474.05, CSIRO H5474.06, CSIRO H5474.07, CSIRO H5474.08, CSIRO H5474.09, CSIRO H5474.10, CSIRO H5474.11, CSIRO H5474.12, CSIRO H5474.13, CSIRO H5476.01[e], CSIRO H5476.02[e], CSIRO H5476.04, CSIRO H5476.05, CSIRO H5476.06, CSIRO H5476.07, CSIRO H5584.01, CSIRO H5584.02, CSIRO H5584.03, CSIRO H5584.04, CSIRO H5584.05, CSIRO H5584.06, CSIRO H5584.10, CSIRO H5612.01, UMS MMKK24[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H4926.09, CSIRO H4926.10 (Nakhon Si Thammarat, Thailand); CSIRO H4927.05, H4927.07 (Trang, Thailand); MNHP A-7920[c] (India); MTUF 30004 (Thailand); NMV A949 (possible syntype of *Trygon macrurus* Bleeker 1852) (Indonesia); RMNH 2460[c], RMNH 2468[c], RMNH 2469[c], RMNH 7438(1)[c], RMNH 7438(2)[c], RMNH 7442(1)[c] (syntype 1of3) ('East Indies'); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia); RMNH 7442(2)[?] (syntype 2of3), RMNH 7442(3)[?] (syntype 3of3)('East Indies'); UMS MMSK(c7)[e,?], UMS MMSK(c8)[e,?] (Sandakan, Sabah, Malaysia).

Himantura gerrardi: var 'large denticle' —
CSIRO H4919.02, CSIRO H5479.05, CSIRO H5479.06, CSIRO H5479.07, CSIRO H5479.11 (Sandakan, Sabah, Malaysia); CSIRO H4918.02[a], CSIRO H5482.04, CSIRO H5482.05, UMS MMT1[e], UMS MMT5, UMS MMT10 (Tawau, Sabah, Malaysia); CSIRO H5484.02, CSIRO H5484.03, CSIRO H5484.04, CSIRO H5484.05, CSIRO H5484.06, CSIRO H5484.07, CSIRO H5617.02, CSIRO H5617.03, CSIRO H5617.04, CSIRO H5617.05, CSIRO H5618.01[?] (Semporna, Sabah, Malaysia).

Himantura jenkinsii (Annandale 1909)

Jenkins whipray

Figures 3.2.5e-f, 3.2.6i, 3.2.7g-h, 3.2.8g-h, 3.2.9d, 3.2.10c-e, 3.2.11h, 3.2.12d-e, 5.2.9–5.2.10; Tables 5.2.5–5.2.6

Trygon jenkinsii Annandale 1909: 28, fig. 4, 4a (original description, illustrated). Holotype: dried skin and mouth preserved in spirit, both registered as F 2437/1 in the Indian Museum (Madras), 103.75 cm disc width, mature male (caught with another mature male). Type locality: Ganjam coast, India in 23 to 27 fathoms (41-49 m depth) during March 1909.

Synonymy. —

Dasybatus (Himanturus) jenkinsii: Garman 1913, 378 (description after Annandale).

Amphotistius (Dasyatis) jenkinsii: Fowler 1941, 432 (description after Annandale).

Dasyatus jenkinsii: Morrow 1954, 803 (brief description). Locality: Shimoni, Kenya.

Himantura draco Compagno & Heemstra 1984: 6, figs.1-8 (original description based on an immature male, figured, illustrated). Holotype: RUSI 996, 561 mm disc width, immature male. Type locality: vicinity of Durban, Natal, S. Africa, probably in water less than 50 m deep.

Himantura sp.1: Michael 1993, 87 (brief account, figured, misidentification).

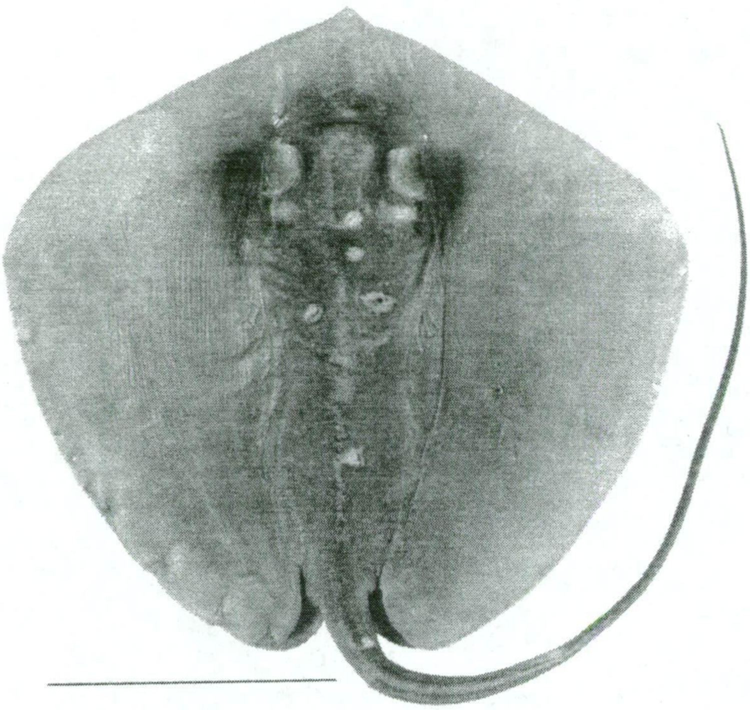
Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, trunk robust; snout moderately long, apical lobe pointed and distinct; lateral apices moderately angular, anterior disc margin slightly concave to straight. Orbits large. Dorsal surface of disc yellowish-brown, ventrally white. Tail dark grey to blackish posterior of sting; ventral base mottled dark grey except for a pale, narrow medial area. Secondary denticle band extending along trunk from interorbital to tail base, constricted above head region; semi-erect wedge-shaped thorns in 1-2 independent rows extending posteriorly from centre of disc along midline of trunk and tail; denticles on tail imbricated.

Description. — Disc rhomboidal, width 1.05-1.14 times length; trunk robust, maximum disc thickness 10-13% of disc width (DW); preorbital snout moderately long, apical lobe pointed and distinct, angle 123-129^{o}; anterior margins of disc straight, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.9-5.2.10). Pelvic fins short, 16.0-18.9% DW; width across base 10.1-11.8% DW; capable of strong forward rotation, often directed laterally. Claspers of adult male (Figs. 3.2.5e,f) long and stout, dorsal surface slightly convex, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, prominent notch anteriorly. Tail stout, slightly longer than disc width, length 1.07-1.39 times disc width; base narrow, subcircular in cross-section, width 0.98-1.47 times height at base.

Snout moderately long, depressed; preoral snout length 3.03-3.64 times mouth width, 2.12-2.44 times internarial distance, 20.2-24.4% DW; direct preorbital snout length 1.47-2.17 times interorbital length, horizontal length 1.37-2.06 times interorbital length; snout to maximum disc width 31.4-37.9% DW; interorbital space flat; eye large, diameter 52-83% spiracle length, orbits protruded, diameter 0.88-1.17 in spiracle length, interorbital distance 1.34-2.35 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak double concavity, length 0.31-0.46 in internasal distance; internasal distance 0.52-0.61 of prenasal length, 2.17-3.19 times nostril length. Nasal curtain skirt-shaped, posteriorly expanded, relatively broad, width 1.74-2.02 times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; oronasal groove prominent; moderately well-corrugated skin on ventral surface of lower jaw confined to narrow strip around lips. Mouth floor with 2-4 short papillae; medial pair simple, knob-like, rounded distally, subequal in size, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair; outer pair small, or absent.

Figure 5.2.9. Representative specimen of *Himantura jenkinsii* in dorsal and ventral views. SUML BRU116 (231 mm DW; immature male; Palawan, Philippines). Photos by T. Carter. Bars 10 cm.



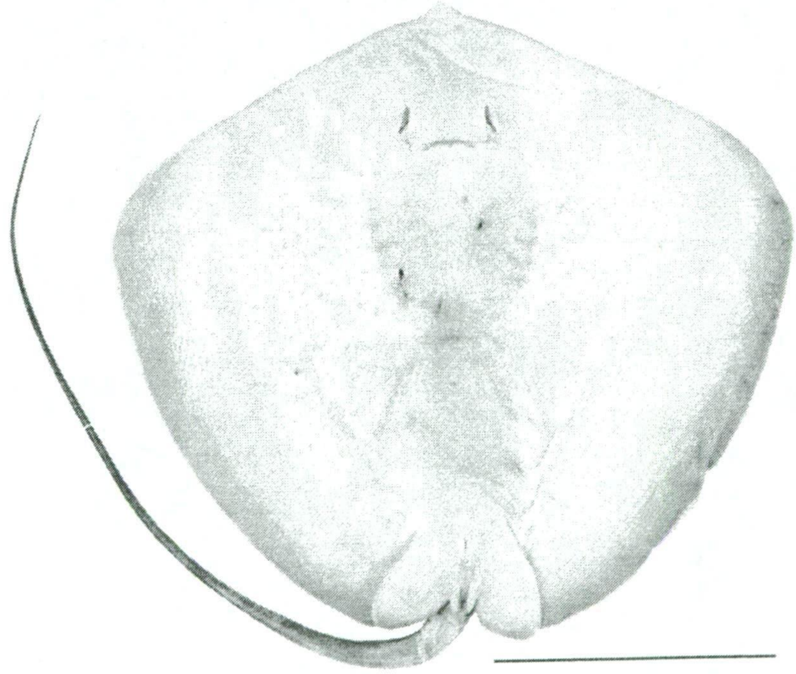
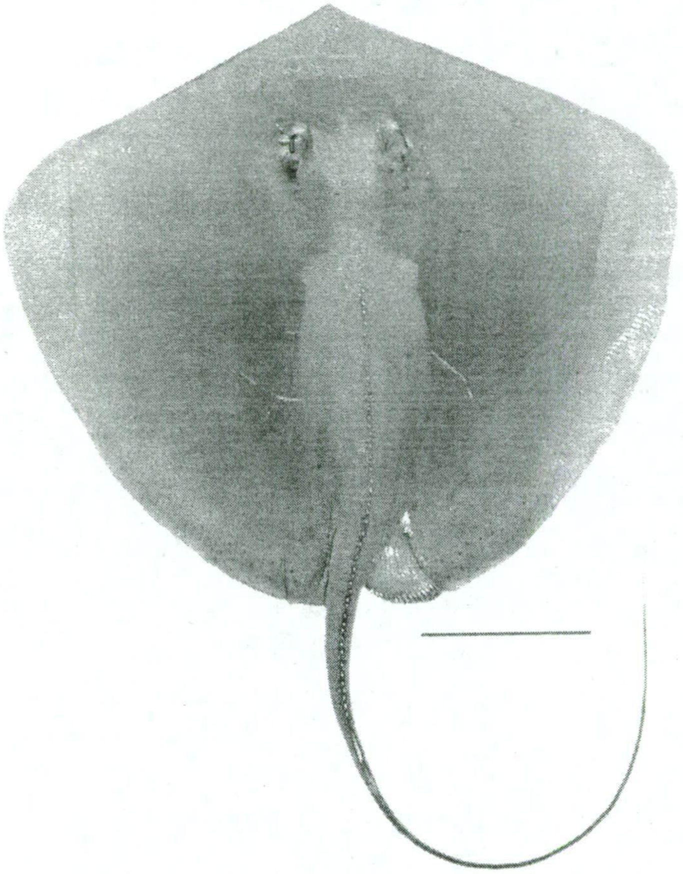
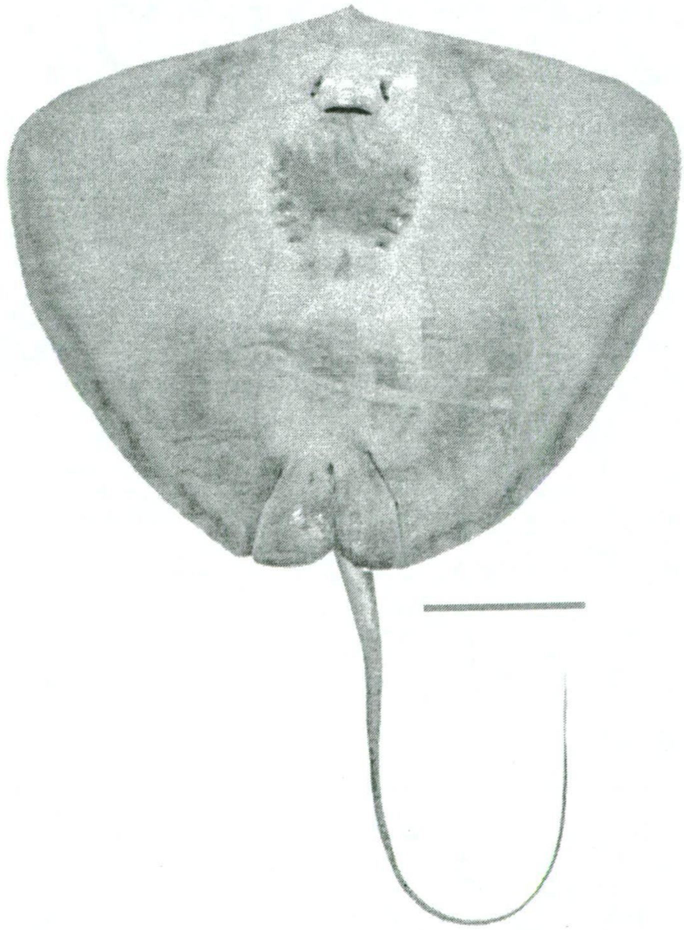


Figure 5.2.10. Representative specimen of 'spotted' *Himantura jenkinsii* in dorsal and ventral views. CSIRO H3375.01 (711 mm DW; female; Gulf of Carpentaria, Australia). Photos by T. Carter. Bars 10 cm.





Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak. Tooth row counts 28 and 31 for upper and lower jaws respectively in holotype of *H. draco* (Compagno & Heemstra 1984); not available from non-types.

Gill opening margins smooth, straight; length of first gill slit 1.22-1.55 times length of fifth, 0.36-0.50 of mouth width; distance between first gill slits 1.72-1.97 times internasal distance, 0.39-0.43 of ventral head length; distance between fifth gill slits 1.09-1.20 times internasal distance, 0.24-0.26 in ventral head length.

Squamation. — Stages of squamation with broad size ranges, with Stages 1, 2 and 3 including tail denticles simultaneously developing. Development of denticles on tail faster compared to on the disc.

Holotype in early part of Stage 4: its dorsal surface with a well-developed subrectangular denticle band. Denticle band width confined to within the interspiracular distance; consisting of small, flat, round denticles, which gradually become smaller towards the periphery, and a single row of stout, short, retroverted spines with flat bases, extending from scapular region to base of the anterior stinging spine. Pectoral and pelvic fins naked; tail covered with small, bluntly spinous tubercles (Annandale 1909).

Stage 0: from birth (ca. 230 mm DW) (Fig. 5.2.9) — Disc entirely smooth, without suprascapular denticles. In a later part of the stage (ca. 284 mm DW), initial denticles (3.21 mm) appear scattered around suprascapular. Denticles cone-shaped, base evenly rounded; fine barely visible with naked eyes.

Stages 1-3: (ca. 395-520 mm DW) — Development of primary median denticle band above first synarcual, simultaneous with initial development of discontinuous secondary denticle patches on head and scapular, and of independent (1-3) rows of enlarged, wedged-shaped denticles along midline of trunk and tail. Primary band developing as several (2-3) rows of closely spaced to imbricated, flat and narrow heart-shaped denticles, the base entirely embedded in skin.

Secondary band adjacent median independent rows of enlarged denticles, laterally expanded at midscapular region; lateral extension with truncated anterior margin, pointed apices, and broadly convex posterior margin, forming a fork-like band shape. Denticles closely set, imbricated; largest (4.3 mm) along mid-trunk, gradually decreasing towards band margin. Denticle band margin well-defined. Development of secondary band simultaneous with those on the tail.

Stage 4: (>520 mm DW) (Fig. 5.2.10) — Secondary denticle band well-developed, continuous along trunk and tail; irregular, margin well-defined; anteriorly extended to just in front of orbits in largest specimen (912 mm DW; CSIRO H2906.01), naked snout ratio 99.3-171.0%. Band generally convex, but strongly constricted above first synarcual, slightly constricted just after scapular region, and indented anterior of pectoral fin insertion, before gradually narrowing towards tail base, becoming as wide as tail base; continuing postero-ventrally and enveloping entire tail beyond tail base.

Primary denticle band becomes obsolete at this stage.

Wedged-shaped denticles along mid-trunk particularly largest; flat and spinulous denticles interspersed, present on all surfaces of tail behind sting.

Stage 5: (>910 mm DW) — Development of tertiary denticle band outside secondary band; denticles minute, granulous, widely-spaced and evenly distributed.

Stage 6 not applicable for this species.

Holotype with two serrated stinging spines. Specimens examined (n=8) with one elongate stinging spine, except in a large adult (520 mm DW, CSIRO CA3947) three stings present.

Meristics. — Total pectoral-fin radials 145-151 (n=6); propterygium 56-60, mesopterygium 19-23, metapterygium 66-71; pelvic-fin radials 24-30 (n=6);

vertebral segments 117-125 (n=4), monospondylous 45-49 (n=5), prespine diplospondylous 70-74 (n=4) and no postspine diplospondylous (n=6).

Colour. — Dorsal surface of disc yellowish-brown dorsally when fresh; colour plain, except for dark dendritic markings of the sensory pore openings on snout and on outer margin of pectoral fins. Specimens obtained from off South Africa (including holotype of *H. draco*), Sri Lanka and northern Australia, have small black spots diffused along the dorsal posterior margin of the pectoral-fins. Ventral surface of disc and pelvic fins uniform white, sometimes with narrow band of light-grey on margin beginning apex of pectorals; margin behind mouth pinkish. Tail yellowish-brown dorsally between tail base and sting base, dark grey to blackish posterior of sting. Ventral surface of tail base of both young and adults, mottled, except for a narrow pale (whitish) patch along mid-region to sting base.

Skeletal morphology. — Neurocrania of two female specimens, 492 mm DW (Figs. 3.2.7g, 3.2.8g), and 395 mm DW (Figs. 3.2.7h, 3.2.8h) with elongate nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval; distinctive keyhole-shaped anteroposterior fontanelle, which extends to level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate, with rounded tips, and base broad triangular; supraorbital crests low, slightly concave along orbital margin; sphenopterotic ridge a narrow ledge with straight margins; lateral commisure moderately broad.

Scapulocoracoid of 492 mm DW female, a mature male (disc width not available), and 395 mm DW female (Figs. 3.2.10c-e) relatively broad, moderately high, posterior part moderately extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a modeately large postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle moderately high and long, 2.5 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle of 492 mm DW female (Fig. 3.2.11h) broadly arched, relatively thin, median prepelvic process absent, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium of a mature male (disc width not available) (Figs. 3.2.12d-e) relatively simple; 2 basal segments; beta cartilage present as a separate element, merging posteriorly with axial cartilage; dorsal marginal cartilage broad, spoon-shaped, posterior edge merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, suboval rectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of mixopterygial tip, and narrowly extending to lateral surfaces.

Size. — Birth size around 230 mm DW; length at first maturity (males) between 750 and 850 mm DW. A 650 mm DW male specimen (CSIRO H3649.01) was determined as being an adolescent (maturity stage 3), while another male specimen (CSIRO H2906.01) 912 mm DW, as mature (maturity stage 4). The holotype of *H. jenkinsii*, 1037 mm DW, is a mature male. A female with disc width 1500 mm from Socotra Islands and from off North West Madagascar have been reported as having empty and reduced uteri (Stehmann 1995).

Etymology. — In honour of Dr. J.T. Jenkins, Scientific Adviser on Fisheries to the Government of Bengal, whom Annandale described as a most zealous coadjutor in the work of the Indian Museum.

Common names. — Jenkins whipray (Last & Stevens 1994).

Distribution. — Wide ranging Indo-West Pacific whipray known from numerous records from southern Africa from less than 50 m depth (Compagno & Heemstra

1984), Andaman Sea to Philippines (Kuiter & Debelius 1994), and to 30 m on shelf off the North West Indian Ocean, Socotra Islands, to 29 m off North West Madagascar (Stehmann 1995).

Comparisons. — Although widely distributed, this species is not well-known. It is closest it *H. fai* (Jordan & Seale 1906), but is distinguished from the latter, and from all other Indo-Pacific *Himantura*, particularly in its unique squamation, i.e. the presence of several rows of enlarged semi-erect wedged-shaped thorns along the trunk and dorsal midline of tail. Dissimilarities of the neurocranial features between *H. jenkinsii* and *H. fai* are noted in the species description of *H. fai.*

Remarks. — Annandale (1909) noted this species as resembling *Trygon akajei* (= *Dasyatis akajei*), or even identical to *T. dadong* Bleeker (1856). However, he also noted several differences from the former, particularly in the size, proportions of the disc and tail, lepidosis (=squamation) and character of the teeth and jaws, and provided some direct measurements of specimens of what he considered as six allied species, *T. uarnak, T. gerrardi, T. favus, T. bleekeri, T. alcockii* and *T. jenkinsii* to facilitate comparison.

A very similar nominal taxon *H. draco* Compagno and Heemstra (1984) is treated as a junior synonym herein. Compagno and Heemstra noted the species they described differs from *H. jenkinsii* in its colouration, preorbital snout length, pelvic-fin size and length, and in denticle shape. They also considered earlier reports of *H. jenkinsii* in the western Indian Ocean as likely to be misidentification of *H. gerrardi*. Stehmann (1995), whom reported two new records of the species from the western Indian Ocean later supported this.

Compagno *et al.* (1989) also claimed that *H. draco* is endemic in East Coast off Durban. However, since Compagno and Heemstra (1984), and Stehmann (1995), there have been more reports of whiprays resembling *H. jenkinsii* in form but which have dark spots along the posterior margin of the disc. Examples are quoted from the Arafura Sea (Last & Stevens 1994), and from western Sri Lanka (Morón *et al.* 1998).

Morphological and meristic data, as well as comparison of the skeletal structures of *H. jenkinsii* and *H. draco* show that the data for these two colour morphs are overlapping (Tabs. 5.2.5–5.2.6). It is further noted that the holotype of *H. draco* is an immature male specimen, 561 mm DW, with developing characters, particularly squamation characteristics.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last in after respective localities). Type specimens are indicated.

CAS 213283, CAS 213284, CAS 213286(1of3), CAS 213286(2of3) (Thailand); CSIRO CA3947, CSIRO H4004.05[b] (north of Legendre Island NW shelf, WA, Australia); CSIRO H2906.01[a] (north of Hopeful Bay, Marchinbar Island, Arafura Sea, NT, Australia); CSIRO H3375.01, CSIRO H3622.01[a], CSIRO H3649.01(west of Weipa, Gulf of Carpentaria, Australia); CSIRO H4123.02 (Sri Lanka); CSIRO H4918.01 (Tawau, Sabah, Malaysia); CSIRO H5475.01[a,e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H5585.01[b] (off Beruwela, Sri Lanka); SUML BRU116, SUML JPAG213[e] (Philippines).

Himantura toshi Whitley 1939

Toshs whipray

Figures 3.2.5h-n, 3.2.6m, 3.2.7k-r, 3.2.8k-q, 3.2.9g, 3.2.10i-o, 3.2.11l-n, 3.2.12g-i, 5.2.11–5.2.12; Tables 5.2.7–5.2.8

Himantura toshi Whitley 1939: 258 (original description based on single preserved specimen, and illustration by Dr. J.R. Tosh). Holotype: AMS IA.39, 294 mm disc width, immature male. Type locality: Clarence River estuary, New South Wales, Australia; November 1903.

Synonymy. —

Dasyatis uarnak (not Forsskål): Tosh 1903, 20, pl. v, fig. 2 (brief description, illustrated, misidentification). Locality: Moreton Bay, Queensland, Australia.

Dasyatis uarnak (not Forsskål): Stead 1907, 2 (description based on an immature male specimen 305 mm disc width which was received in November 1903, from Clarence River estuary, New South Wales, Australia; misidentification; specimen later designated as holotype for *Himantura toshi* by Whitley [1939]).

Himantura uarnak (not Forsskål): McCulloch 1934, 12, pl. iii, fig. 38a (listed, misidentification). Locality: Clarence estuary, New South Wales, Australia.

Himantura toshi: Whitley 1940, 211, figs. 240 and 241 (description, misidentification in part). Localities: Moreton Bay; Broome; Bedwell Point, Northern Territory, Australia.

Himantura uarnak (not Forsskål): Marshall 1966, pl. 2(1) (listed, 300 mm disc width, misidentification). Locality: Great Barrier Reef, Australia.

Himantura uarnak (spotted form) (not Forsskål): Sainsbury *et al.* 1985, 51 (figured, 230 mm disc width, misidentification). Localities: Northern and Northwestern Australia.

Himantura uarnak (not Forsskål): Gloerfelt-Tarp & Kailola 1984, 38, fig. 1 (brief description, illustrated, misidentification of juvenile in part). Locality: Northwestern Australia (Northwest Cape to Timor Sea).

Himantura uarnak (juvenile) (not Forsskål): Grant 1987, 45 (figured, 300 mm disc width, misidentification). Locality: Australia.

Himantura sp. A: Last & Stevens 1994, 397, fig. 40.9, pl. 67 (misidentification). Locality: tropical eastern and northern Australia in coastal habitats.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, trunk moderately flat. Dorsal surface diffused with black or dark brown spots or specks, spots extending onto tail until sting base; distance between spots more than diameter of largest spot apart. Tail banded beyond sting in both young and adults. Prominent primary denticle band throughout its life stages. Secondary denticle band subrectangular, with well-defined margin; band extending along trunk from preorbital to tail base, its width confined to interspiracular distance; band fully developed by 300 mm disc width.

Description. — Disc rhomboidal, width 1.12 times length in holotype (1.00-1.24 in other nontype materials); moderately flat, centre raised slightly at midscapular (more pronounced in larger specimens), maximum disc thickness 11% (8-13%) of disc width (DW); preorbital snout moderately long, broadly triangular, without obvious medial lobe at the snout tip (small medial lobe sometimes present), angle 112^{o} (100.5-118^{o}) (no particular trend in snout angle observed for juvenile and adults, or between the sexes); anterior margins of disc weakly concave (rarely to almost straight in some juveniles), lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.11-5.2.12). Pelvic fins short, 16.6% (16.1-19.0%) DW; width across base 10.5% (9.0-12.1%) DW. Claspers of adult male (Figs. 3.2.5h-n) long and stout, dorsal surface slightly convex, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle short, about 1/3rd of clasper length on its outer margin, without prominent anterior notch. Tail slender and whiplike, tapering gently evenly toward sting and with very weak taper beyond sting to tail tip, length 2.23-3.30 times disc width; base narrow, subcircular in cross-section, width 1.22 (0.94-1.42) times height at base, slightly depressed in large individuals more than 380 mm DW; depressed distally (almost twice as wide as high near tip); deep longitudinal groove on ventral surface (under the sting), and a low ridge along lateral surfaces originating near distal tip of sting to tip of tail (in all specimens examined, including holotype).

Snout moderately long, depressed; preoral snout length 3.53 (2.61-3.63) times mouth width, 2.30 (2.03-2.57) times internarial distance, 22.8% (18.4-25.4%) DW;

direct preorbital snout length 1.90 (1.17-1.96) times interorbital length, horizontal length 1.76 (1.11-1.81) times interorbital length; snout to maximum disc width 37.4% (33.2-46.5%) DW; interorbital space flat; eye moderately large, diameter 77% (44-93%) spiracle length; orbits slightly protruded, diameter 1.39 (0.70-1.37) times spiracle length, interorbital distance 1.57 (1.39-2.66) times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils narrow, laterally expanded, outer margin with a weak double concavity, length 0.53 (0.33-0.58) in internasal distance; internasal distance 0.58 (0.54-0.65) of prenasal length, 1.90 (1.74-2.36) times nostril length. Nasal curtain relatively narrow, width 1.61 (1.30-1.83) times length, lateral margin almost straight, weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave to weakly double concave.

Mouth arched; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 4 well-developed papillae; medial pair simple, rounded distally, often bifurcated to its base, longitudinally flattened, sub-equal in size and larger than outer pair, closer to each other than outer two; outer pair located at each corner of mouth, widely separated from inner pair.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak. Tooth rows 21-29 in upper jaw, 21-33 in lower jaw (not including holotype).

Gill opening margins smooth, straight; length of first gill slit 1.67 (1.03-1.89) times length of fifth, 0.45 (0.28-0.46) of mouth width; distance between first gill slits 1.74 (1.60-1.89) times internasal distance, 0.40 (0.36-0.50) of ventral head length; distance between fifth gill slits 1.08 (0.96-1.36) times internasal distance, 0.25 (0.22-0.32) in ventral head length.

Squamation. — Stages of squamation with broadly overlapping size ranges, tail covered with denticles especially in adults. Development of primary denticle band simultaneous with centre of disc appearing slightly raised.

Holotype in early part of Stage 2 (Fig. 5.2.11): its dorsal surface mainly smooth, with primary denticle band above first synarcual, and patches of secondary denticles on head and on mid-dorsal region from end of cranium to rear of scapular; with two suprascapular denticles. Denticles in primary band flat, ovate to heart-shaped; pronounced, dense and abutted. Denticles in secondary patches pointed conical, minute and widely spaced. Suprascapular denticles flat, heart-shaped (length of first and second denticle 2.92 and 2.56 mm respectively). Tail naked before sting, denticles present after sting; denticles short, bluntly pointed subconical; widely spaced. Ventral surface of disc and tail naked.

Stage 0: from birth (ca. 140-230 mm DW) (Figs. 5.2.12a) — Disc entirely smooth. Suprascapular denticle(s) appearing during late-stage; initially weakly evident and entirely covered with skin, soft when first exposed, numbering between 1-3 denticles; becoming hardened with age, increasing in size (length of largest denticles ranging between 1-4 mm), and more pronounced in shape (seed-shaped to narrow heart-shaped).

Stage 1: (ca. 200-310 mm DW) — Development of primary denticle band above first synarcual adjacent suprascapular denticles. Band initially develop in a single row, later flanked by additional rows, before finally forming a weak 't'-shape band in final part of the stage. Denticles flat ovate to narrow heart-shape, closely set, abutted; subequal in size (median row slightly larger than those adjacent, but smaller than suprascapular denticles).

Stage 2: (ca. 260 mm DW) — Initial stage for development of discontinuous secondary denticle patches; onset on dorsal surface of tail behind sting, followed by simultaneous development of cranial (interorbital above fontanelle, and inner margin of spiracles behind orbits), and scapular patches; scapular patch particularly with well-defined margin. Denticles in cranial and scapular patches with flat crowns, varying from ovate to heart-shape; on inner margin of spiracles conical, base rounded to weakly stellate; on tail, bluntly pointed, varying in shape from subconical to conical; appearing scattered and well-spaced; minute, smaller than suprascapular and primary denticles.

Figure 5.2.11. Holotype of *Himantura toshi* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of primary denticle band; d, close-up of oronasal; e, pelvic-fins and cloacal region. AMS IA39 (294 mm DW; immature male; Clarence River estuary, New South Wales, Australia). Photos by T. Carter. Bars 10 cm.

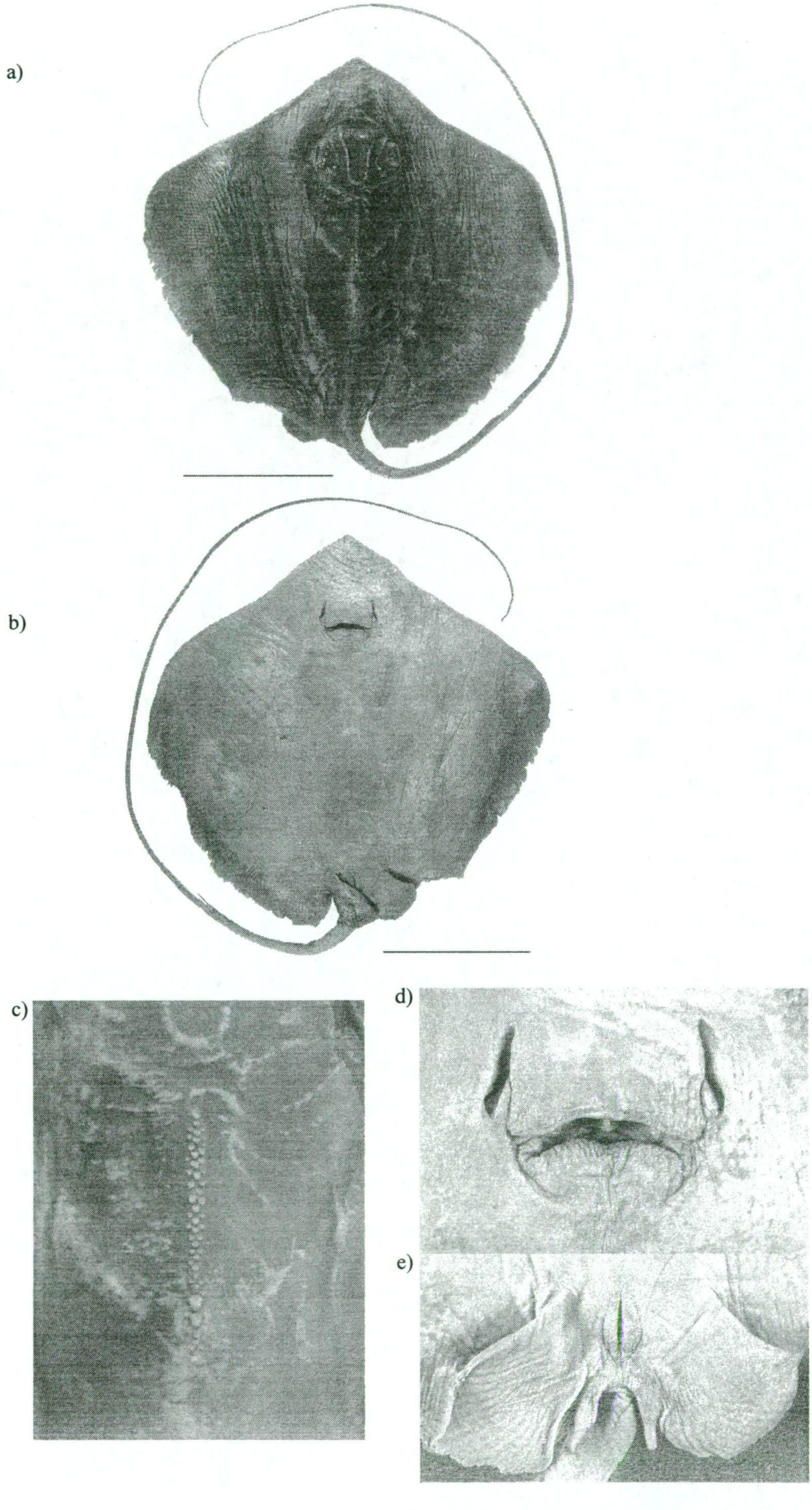
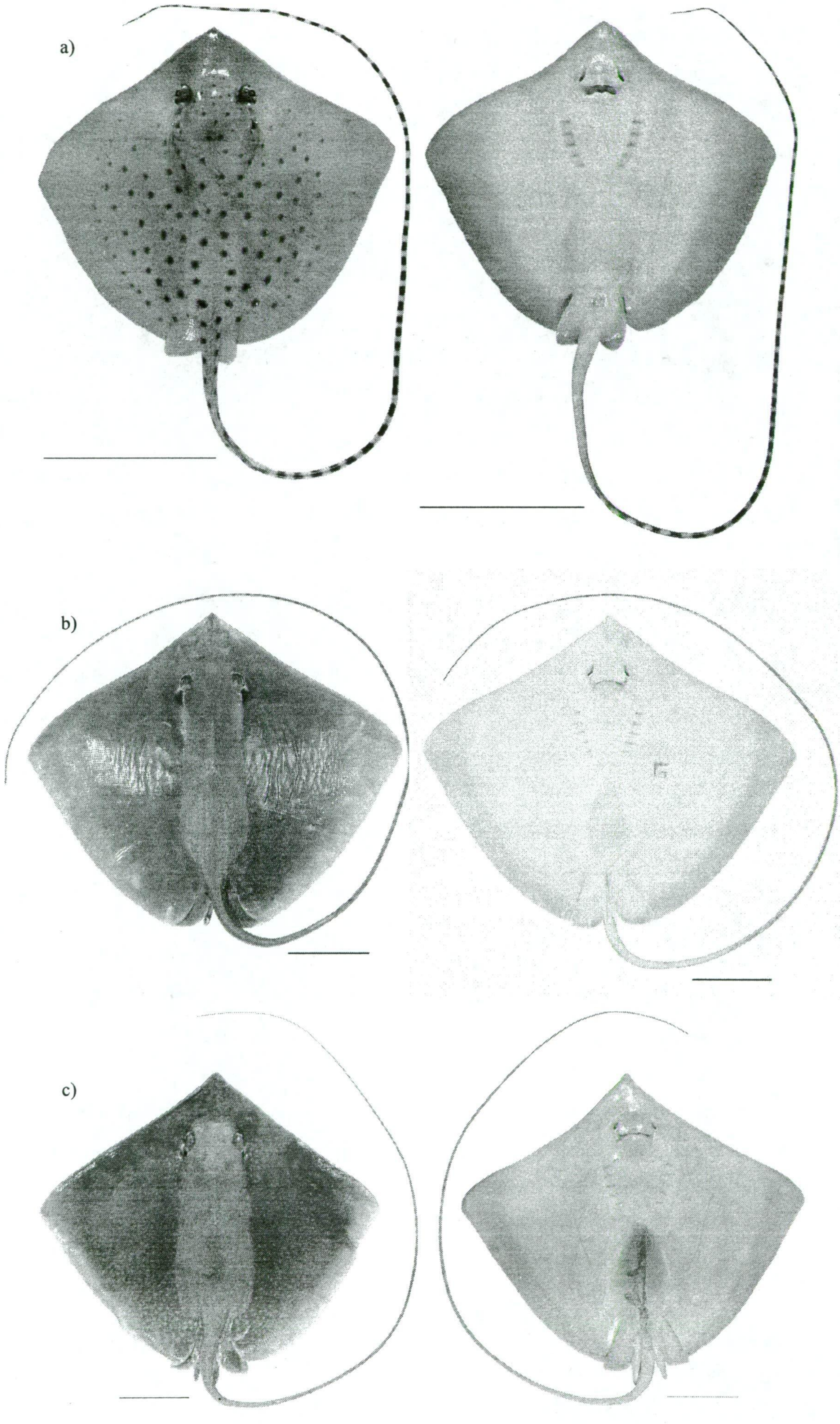

a)
b)
c)
d)
e)

Figure 5.2.12. Representative specimens of *Himantura toshi* indicating squamation and intraspecific colour variation in dorsal and ventral views. a, 210 mm DW (CSIRO H1464.4; female; North-West Shelf, Western Australia, Australia); b, 301 mm DW (CSIRO H5204.01; immature male; Northern Territory, Australia); c, 507 mm DW (CSIRO H1220.01; mature male; Gulf of Carpentaria, Australia). Photos by T. Carter. Bars 10 cm.



Primary denticle band remain prominent at this stage.

Stage 4: (ca. 300 mm DW) — In early part of this stage (320–350 mm DW), cranial and scapular denticle patches weakly coalesce through a scattering of widely spaced median connective denticles. Denticles similar in shape and size to those in adjacent patches. A maturing male specimen (CSIRO H5204.01) 301 mm DW is in late-stage, with a well-developed denticle band (Fig. 5.2.12b).

Mid-stage (330–380 mm DW), cranial and scapular patches connected through a narrow band of connective denticles, forming a continuous, irregular longitudinal secondary band, but discontinuous with those on tail; band widest above scapular, constricted over nape; anteriorly following outline of fontanelle, its anterior margins adjacent orbits. Band varying in shape above scapular, from distinctive leaf-shape to rectangular; posteriorly, converging sharply above pectoral-fin insertion. Denticle patch on inner margin of spiracles barely developing, patch weakly triangular-shaped on antero-dorsolateral surface. On tail, denticles reaching just anterior of sting base on dorsal and dorsolateral surfaces, becoming dense anteriorly; sparse on last 1/3rd of caudal, with smaller similar-shaped denticles resembling those of disc.

Late-stage (>380 mm DW), secondary denticle band well-developed, continuous along trunk and tail; subrectangular, margin well-defined; anteriorly extended to just in front of orbits, naked snout ratio 65-110%; slightly constricted above first synarcual; slightly expanded above abdominal region, diverging laterally for a distance equivalent to a spiracle length at pectoral-fin insertion; extending on to tail, across almost entire dorsal half, ventral surface of tail base naked.

Denticles most dense along median dorsal, comprising small, flat, ovate to heart-shape denticles, and interspersed with small conical denticles with scalloped bases; abutted denticles extend over tail, becoming sparse towards tail tip, absent ventrally and at tail tip.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine, second sting rarely present. Second sting similar in shape and size to first sting, grows above first sting during late part of Stage 2 of squamation.

Meristics. — Total pectoral-fin radials 132-134 (139-136, n=13); propterygium 51 (48-50), mesopterygium 16-18 (19-24), metapterygium 63-67 (58-65); pelvic-fin radials 24 (20-29, n=13); vertebral segments 98 (94-105, n=43), monospondylous 44-52 (n=8; count for holotype not available), prespine diplospondylous 47-55 (n=8; count for holotype not available) and postspine diplospondylous absent in all specimens, including the holotype.

Colour. — Dorsal surface of holotype almost uniformly dark brown with paler abraded areas (presumably through preservation), margins lighter in colour, no evidence of spotting; ventral surface paler and plain; tail beyond sting with a faint evidence of alternating light and dark banding, bands with similar width.

Fresh specimens greenish grey to greyish brown, usually diffuse with dark (brown to black) spots dorsally, rarely with fuzzy white spots; posterior edges of the disc paler and pinkish; tail banded beyond sting in both young and adults; ventral surface of disc and pelvic fins uniformly white. Several more-recently preserved specimens indicate dark brown dorsal disc surface colouration, but paler than holotype, and dark spots and bands on tail remain visible.

At birth, posterior margin of disc plain and lighter tone than rest of disc, except on the free rear tip, a few dark spots often extend here; spots with fuzzy edges in neonatals, becoming distinct and darker with age. Young specimens (150 - 200 mm DW) greyish to light brown, with light brown to blackish (dark brown) spots either distributed over the entire dorsal disc surface, including the pelvic fins, or confined to the posterior portion of the disc. In males, the dorsal surface of the claspers dark brown colour than rest of pelvic fins. Larger specimens (from 200 mm DW) usually with fine spotting on their heads, including the orbits and snout; spots extending onto dorsolateral surface of tail from base to sting base. Floral patterns occasionally present in mature adults (one specimen had only white spots, Fig. 5.2.12c); the darker spots surrounded by 3-4 smaller or similar sized whitish spots; the edges of the spots well-defined or fuzzy; the dark spots may extend onto the lateral side of the tail with the white spots becoming faded; beyond the sting, dark ocelli forms on the dorsal surface of the tail, forming a banding patterning of the tail when viewed laterally. In large adults, the banding on the tail becomes fine, forming a reticulate patterning; lower half of the tail white.

Strong intraspecific variation in dorsal disc spotting pattern; spots generally distributed over entire disc surface, but may be confined to posterior surface around the tail base, or entirely absent. More commonly observed are individuals with uniform-sized spots over entire disc surface; the distance between the spots (always) wider than the diameter of each spots; the size of spots on a single individual may vary, the smallest smaller than the size of its pupil, resembling a speck, whilst the largest may be slightly larger than its pupil; large and small spots often intersperse, but larger spots are generally located on the posterior part of the disc, gradually becoming smaller anteriorly and towards the disc margin.

Skeletal morphology. — Neurocrania of eight specimens, a female and males ranging from juveniles to mature (disc widths not available) (Figs. 3.2.7k-r, 3.2.8k-q) with moderately elongate and large nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval, internasal moderately broad; fontanelle triangular-shaped, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen anteroventral optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate and robust, basally triangular and posteriorly rounded; supraorbital crests low, slightly concave along orbital margin; sphenopterotic ridge a narrow ledge with straight margins; lateral commisure moderately broad.

Scapulocoracoid (Figs. 3.2.10i-o) relatively broad, moderately high, posterior part moderately extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; 1-3 small postdorsal fenestrae; a small fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra evenly concave. Procondyle moderately long, 2.5 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Figs. 3.2.11l-n) broadly arched, relatively thin, median prepelvic process absent, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium (Figs. 3.2.12g-i) relatively simple; 2 basal segments; beta cartilage present as a separate element, merging posteriorly with axial cartilage; dorsal marginal cartilage broad, spoon-shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, suboval rectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, and narrowly extending to inner lateral surface.

Size. — Birth size around 143 mm DW; length at first maturity (males) around 500 mm DW. A 480 mm DW male specimen (CSIRO H4083.01) was determined as being an adolescent (maturity stage 3), while two other male specimens (CSIRO H1222.1 and CSIRO H1220.01) 507 and 509 mm DW respectively, as mature (maturity stage 4). Females reaching to around 480 mm DW, as based on two specimens (CSIRO H4083.01 and CSIRO H3329.01) from Western Australia and Queensland respectively.

Etymology. — In honour of (the late) Dr. James R. Tosh, Marine Biologist to the Queensland Govt., and later Professor of Biology at St. Andrew's University.

Common names. — Toshs whipray; Black-spotted whipray (Last & Stevens 1994).

Distribution. — Widely distributed throughout tropical Australia in 10-140 m (Last & Stevens 1994), including the Timor Sea (i.e. specimen with registration CSIRO CA1245 misidentified as *H. uarnak* by Gloerfelt-Tarp & Kailola 1984), and south of Papua New Guinea, down to New South Wales (Clarence River estuary).

Comparisons. — *Himantura* sp. A sensu Last and Stevens (1994), is herein synonymized with *H. toshi*, based on a combination of external and internal characters (i.e. colour, morphometric ratios, squamation, and skeletal structures - particularly the scapulocoracoid). Both *H. toshi* specimens, and specimens tentatively identified as *H.* sp. A (P. Last, pers. comm.) examined, displayed a prominent primary denticle band, consisting of 2-3 acute heart-shaped mid-scapular denticles. Last and Stevens suggested the two as separate species based on their known distribution (i.e. *H.* sp. A is a common inshore over muddy bottoms on mangrove flats, whereas *H. toshi* is more common in the Gulf of Carpentaria), and respective maximum size of the disc width. It is noted that a wide selection of *H. toshi* specimens representing newborns to adult stages was examined, whereas specimens tentatively identified as *H.* sp. A were fewer and limited (less than 5 specimens examined). Unfortunately, efforts to obtain tissue samples for DNA sequence analysis from *H.* sp. A were unsuccessful.

Newborns and immatures are very similar in disc shape (with meristics overlapping), and in disc and tail colouration, to other species of the uarnak complex, particularly to *H. gerrardi* and *H. uarnak.* The snout angle of *H. toshi* is narrowest among the three, ranging between 100-118^{O} (108-124^{O} in *H. gerrardi*; 115-129^{O} in *H. uarnak*), and the distance between each spot closer (less than diameter of largest spot) in *H. uarnak.*

Himantura toshi also differ from *H. gerrardi* in squamation (primary denticle band present in former), and in the structure of their scapulocoracoid (i.e. number of the postdorsal fenestra varying from 1-3, and size smaller, even with a single postdorsal fenestra, in former). Moreover, the rate of denticle band development is slower in *H. toshi*, compared with *H. gerrardi*. As for *H. uarnak*, the mid-scapular denticles are wider, not imbricated; more prominent in young, becoming inconspicuous in very large adults.

Remarks. — *Himantura toshi* was partly misidentified as *H. uarnak* (Forsskål) (illustrated) by Whitley (1940), following which, others have misidentified this species (as quoted in the list of synonyms), and thus reflecting the problem of absence of detailed description for the species. The holotype, quoted by Whitley (1939), was apparently obtained and identified as *Dasyatis uarnak* Forsskål by Stead (1907). According to Stead, it was received in November 1903 from Clarence River estuary. He further noted the species as occurring commonly on parts of the Queensland coast, and that it is very widely distributed. Stead however, suspected this might be a separate species from *H. uarnak*, and suggested a new common name 'banded tailed stingray' based on the banded tail of the specimen he examined, to distinguish it from the 'typical' *H. uarnak*. He also noted the dorsal surface of the disc as spotted.

A specimen from Moreton Bay in Queensland, Australia, figured and identified as *Dasyatis uarnak* by Tosh (1903; see also Whitley 1939), was later reproduced in Whitley (1940), as *Himantura toshi*. Tosh however, remarked the species as 'not as common' as another species (i.e. *D. kuhlii*). He described the specimen as having only one spine on the back, and in front of it (the spine) a small bony ridge - thus apparently referring to the midscapular denticle as the spine; the colour of the dorsal disc surface described as dark brown, with thirty-five bluish white bars on the tail; the tail length twice the body length.

Whitley (1939) noted the holotype as an immature male 305 mm DW or '12 inches across the disc, and disc a little broader than long, tail three times the length of the body'. This specimen has obviously undergone shrinkage as current (1998) measurement indicates 294 mm disc width. Whitley also mentioned about a solitary or single median spine (tubercle, in Whitley 1940) on the specimen, which he probably referred the nuchal or midscapular thorn. Specimens examined in this study usually have two heart-shaped midscapular thorns, including the holotype which also has two.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

AMS IA39 (holotype) (Clarence River estuary, NSW, Australia); CSIRO CA2405, CSIRO CA2406, CSIRO CA4271, CSIRO H312.1, CSIRO H635.1, CSIRO H635.03, CSIRO H635.04, CSIRO H959.1, CSIRO H959.2, CSIRO H959.4, CSIRO H963.1, CSIRO H963.2, CSIRO H963.3, CSIRO H964.1, CSIRO H964.2, CSIRO H3380.01, CSIRO H3380.02, CSIRO H3381.01, CSIRO H3381.02, CSIRO H3381.03, CSIRO H3383.01, CSIRO H3387.01[e], CSIRO H3387.02, CSIRO H3387.03, CSIRO H5204.01, CSIRO H5205.01, CSIRO H5206.01, CSIRO H5586.01, CSIRO H5586.02[b], CSIRO H5586.03[b], CSIRO H5586.04[b], CSIRO H5589.01[b], CSIRO T698, CSIRO T699, CSIRO T700, NTM S.12416.001 (NT, Australia); CSIRO CA1245, CSIRO CA3994, CSIRO H1034.1, CSIRO H1034.2, CSIRO H1464.4, CSIRO H5587.01[b], CSIRO H1041.02, CSIRO H4077.01, CSIRO H4077.02, CSIRO H4077.03, CSIRO H4077.04, CSIRO H4083.01, WAM P29180.001 (NW Shelf, WA, Australia); CSIRO H1220.01[a], CSIRO H1220.2, CSIRO H1222.1[a], CSIRO H1222.2, CSIRO H3322.02, CSIRO H3329.01, CSIRO H3352.01[e], CSIRO H3369.01, CSIRO H3373.01, CSIRO H3373.02, CSIRO H3373.03, CSIRO H3373.08, CSIRO H3373.09, CSIRO H3377.01, CSIRO H3736.01, CSIRO H4421.01, CSIRO H4421.02, CSIRO H4686.01, CSIRO H5588.01[b] (Gulf of Carpentaria, QLD, Australia); CSIRO H2376.01, CSIRO H2376.02, CSIRO H2376.03, CSIRO H2376.04 (Cairns, QLD, Australia); CSIRO H38.1 (Papua New Guinea); CSIRO H4913.02 (West Ajkwa River estuary, Irian Jaya, Indonesia); CSIRO H4914.01 (Minajerwi River estuary, Irian Jaya, Indonesia); CSIRO H3305.17 (E of Shelburne Bay, QLD, Australia); CSIRO H3974.01 (Toondah Harbour, QLD, Australia); QM I12946, QM I20793, QM I22355 (Moreton Bay, QLD, Australia).

Himantura uarnak (Forsskål 1775)

Reticulate whipray

Figures 3.2.3c, 3.2.4c, 3.2.5p, 3.2.6o, 3.2.7t, 3.2.8s, 3.2.9h, 3.2.12j, 5.2.13 – 5.2.16; Tables 5.2.9–5.2.10

Raja sephen var. *uarnak* Forsskål 1775: viii, 18 (original description, not figured, no designated specimens). No types known. Type locality: Red Sea.

Synonymy. —

Pastinachus uarnak: Rüppell 1835, 69, taf. 19, figs. 2a and 2b (description, illustration of dorsal disc and oronasal indicating tooth band in upper and lower jaws). Locality: Red Sea.

Trygon variegatus McClelland 1841: 60 (original description, illustration of a 505 mm disc width mature male illustrated). No types known. Locality: salt-water lake near Calcutta, Bengal Bay, India.

Trygon uarnack: Richardson 1846, 197 (misspelling of *uarnak* Forsskål; listed based on two specimens bequeathed by Hardwicke to the BMNH, one intact (?) specimen in preservative, the other skin only, dried; both specimens not identified). Localities: Sea of China; Indian Ocean; Red Sea; Cape of Good Hope.

Trygon uarnak: Blyth 1860, 44 (description, misidentification in part). Locality: Lower Bengal.

Leiobatus uarnak: Bleeker 1863, 264 (listed). Locality: Atapupu, Timor (=East Timor).

Himantura uarnak: Day 1865, 277 (listed). Locality: Malabar, India.

Trygon (Himantura) uarnak: Günther 1870, 473 (description, misidentification in part). Localities: Indian Ocean and archipelago.

Trygon (Himantura) punctata Günther 1870: 474 (original description based on a young female specimen from Hr. Frank's collection in the British Museum). Holotype: BMNH 1953.8.10.15, 276 mm disc width (measurement by P. Last). Type locality: East Indian Archipelago.

Leiobatis (Himantura) uarnak: Bleeker 1877, figs. a and b, pl. 560, Plagiostom. Pl. 38 (illustration of non-type immature male).

Trygon narnak: Tillier 1902, 318 (misspelling of *uarnak* Forsskål; listed). Locality: Suez Canal, Red Sea.

Dasyatis uarnak: Fowler 1910, 473 (listed). Localities: Padang, Sumatra, Indonesia.

Dasybatus (Himanturus) uarnak: Garman 1913, 376 (description, misidentification in part). Localities: Indian Ocean; Red Sea; East Indies.

Himantura arnak: McCulloch 1929, 29 (misspelling of *uarnak* Forsskål; listed, compiled distribution).

Himantura toshi (not Whitley): Whitley 1940, 212, fig. 240 (description, misidentification in part). Localities: Broome; Gulf of Carpentaria, Queensland, Australia.

Dasyatis (Himantura) uarnak: Fowler 1941, 405 (listed, misidentification in part).

Hymantena narnak: Goeden 1974, 2 (misspelling of *Himantura* Müller & Henle and of *uarnak* Forsskål; listed). Locality: Heron Wistari National Park, Queensland, Australia.

Hymantura uarnak: Myers 1989, 38, fig. 4b (misspelling of *Himantura* Müller & Henle; description, illustrated). Locality: Indo-West Pacific.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, preorbital snout moderately long, broadly triangular, with a small apical lobe, lateral apices moderately angular in young, becoming obtusely angular in adults. Dorsal surface entirely covered with fine dark brown polygonal spots in young, and with broad dark brown reticulations, and/or short narrow irregular bars in adults; spots distributed over a light brown background; bars or reticulations separated by paler (yellowish) narrow lines. Tails of young with a row of dark brown spots on each dorsolateral surface from tail base to sting base; behind sting, tail banded on dorsal and lateral surfaces; otherwise uniformly pale. Dark and pale bands of equal width. Larger specimens and adults, tail with fine dark brown reticulations on a pale (whitish) background, usually becoming blackish towards tail tip, posterior sting. Tertiary denticle band present in large adults.

Description. — Disc rhomboidal, width 1.00-1.10 times length; robust, center raised at mid-scapular, maximum disc thickness 0.10-0.14 in disc width (DW); preorbital snout moderately long, broadly triangular, with a small apical lobe, angle 115-128.5^{o}; anterior margins of disc weakly concave, lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.13-5.2.16). Pelvic fins moderately long, 18.1-23.6% DW; width across base 11.4-14.4% DW. Claspers of adult male (Fig. 3.2.5p) long and stout, dorsal surface slightly convex, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, prominent notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.90-3.48 times disc width; base narrow, subcircular to suboval in cross-section, width 1.09-1.64 times height at base.

Snout moderately long, depressed; preoral snout length 2.34-3.41 times mouth width, 2.23-2.85 times internarial distance, 18.7-22.7% DW; direct preorbital snout length 1.36-1.84 times interorbital length, horizontal length 1.24-1.65 times interorbital length; snout to maximum disc width 33.4-42.6% DW; interorbital space slightly raised; eye moderately large, diameter 30-67% spiracle length; orbits slightly protruded, diameter 0.48-0.89 in spiracle length, interorbital distance 1.81-3.38 times orbit (4.07 in a 940 mm DW specimen). Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak double concavity, length 0.46-0.63 in internasal distance; internasal distance 0.46-0.60 of prenasal length, 1.66-2.12 times nostril length. Nasal curtain skirt-shaped, relatively broad, width 1.76-2.29 times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth arched; shallow oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 4-5 short, well-developed papillae in two transverse rows; medial pair in second row often bifurcated distally, longitudinally flattened, subequal in size, almost three times larger than the single papillae located between them, and than outer pair; single papillae, and outer pair arranged in first row; outer pair located at each corner of mouth, widely separated from single papillae.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth row counts not available.

Gill opening margins smooth, straight; length of first gill slit 1.23-1.59 times length of fifth, 0.33-0.53 of mouth width; distance between first gill slits 2.19-2.58 times internasal distance, 0.40-0.47 of ventral head length; distance between fifth gill slits 1.41-1.68 times internasal distance, 0.26-0.31 in ventral head length.

Squamation. — Stages of squamation with broad overlapping size ranges. With with 2 prominent suprascapular denticles, primary denticle band absent. Rate of squamation relatively fast, secondary denticle band well developed in immatures 500 mm DW.

Stage 0: from birth (ca. 260 mm DW) (Fig. 5.2.16a-c) — Disc entirely smooth. Suprascapular denticles appearing later (ca. 270 mm DW); 1 to 3 (usually 2) ovate to broad heart-shape with convex crown (length of largest 1.8-2.9 mm); distance between suprascapular denticles fairly widely spaced between them, becoming closely set in later part of the stage, but rarely any denticles in between these denticles.

During late part of the stage, 2 to 3 smaller denticles appearing in a row anterior to the suprascapular denticles; denticles small, narrow heart-shaped.

Stage 2: (ca. 275-310 mm DW) — Development of discontinuous secondary denticle patches interorbital and midscapular adjacent the suprascapular denticle(s), and on tail. Patches sparse, irregular, and without well-defined margin. Denticles minute, progressively smaller in size towards margin, mostly embedded in skin, heart-shaped.

As the development progresses (ca. 290 mm DW), the scapular patch extend longitudinally, developing faster than laterally; becoming weakly connected to interorbital patch through a scattering of widely spaced median connective denticles anteriorly, slightly expanded laterally, and extended in a narrow band along the vertebrae, terminating in a point just anterior to pectoral-fin insertion (Figs. 5.2.16e,f).

Denticles uniform flat narrow heart-shape, widely spaced with about half a denticle apart, only slightly decreasing in size towards margin of the patch.

Stage 4: (ca.300 mm DW) (Figs. 5.2.16g-l) — Secondary denticle patches coalesced to form a continuous longitudinal band along the trunk; number of denticles at the nape significantly increasing, forming a broad connection with interorbital patch; posteriorly, rate of denticle development slower, less significant change in band shape from previous stage. Band with moderately well-defined margins.

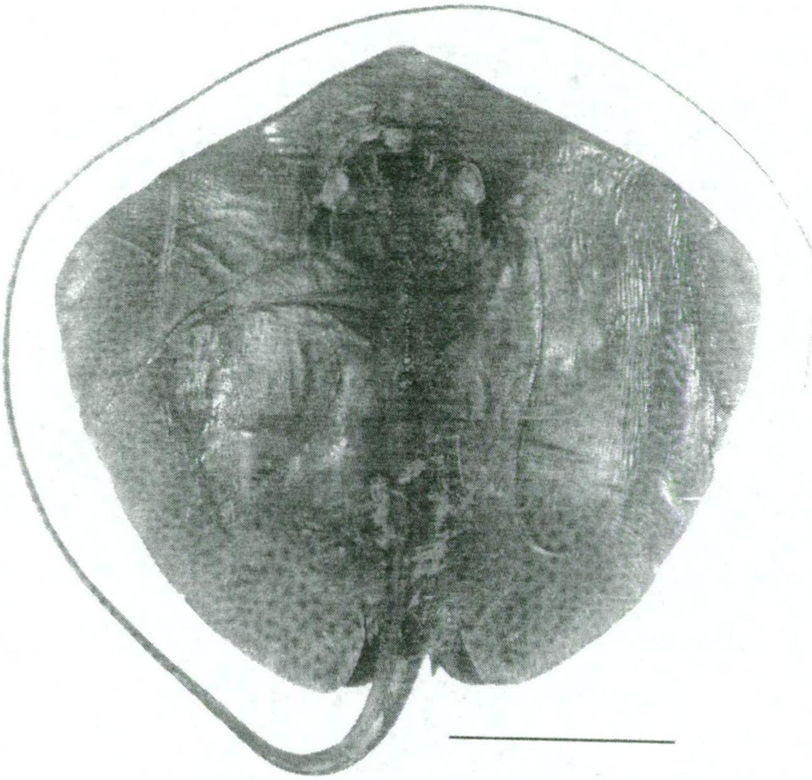
Late stage four, secondary median denticle band well-developed, as a continuous subrectangular longitudinal band with well-defined margin. Band extending to just in front of orbits, naked snout ratio 76-88%; slightly wider than interspiracular width, and slightly constricted at scapular; truncated just anterior of pectoral-fin insertion, narrowing sharply a short distance becoming as wide as tail width at pectoral-fin insertion; band extending strongly onto tail, to sting base.

Denticles in band dense, progressively smaller in size towards margin; small-sized denticles interspersed among larger ones, both with consistent size.

Stage 5: (>1000 mm DW) — Development of small tertiary denticles as loose denticles on the disc outside the denticle band, and further on the snout in very large specimens. Denticles small, granular, evenly distributed.

Stages 1, 3, and 6 not applicable for this species.

Figure 5.2.13. Representative specimen of *Himantura uarnak* in dorsal and ventral views. CSIRO H5484.01 (309 mm DW; immature male; Semporna, Sabah, Malaysia). Photos by T. Carter. Bars 10 cm.



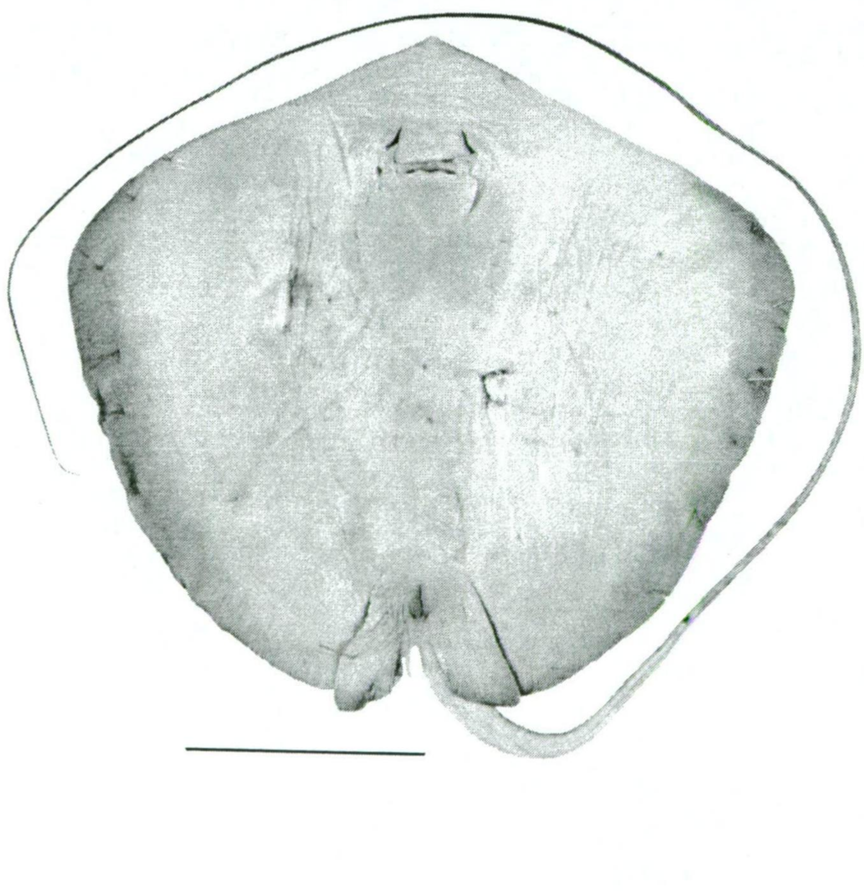
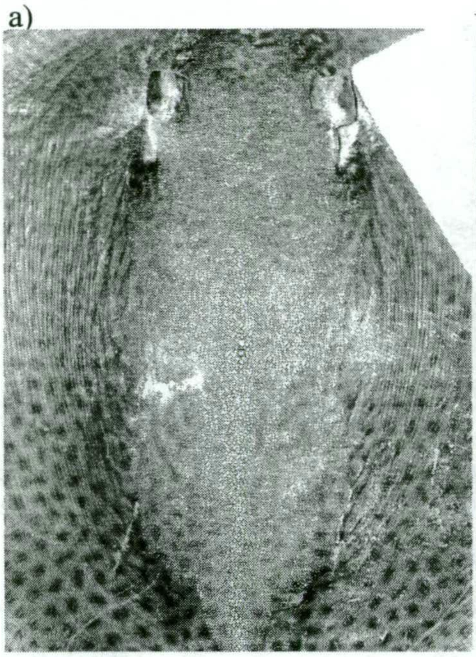
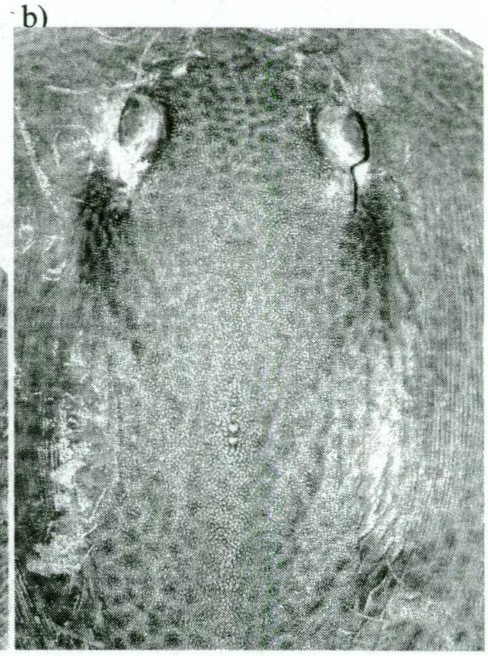


Figure 5.2.14. Representative specimens of *Himantura uarnak* indicating transitional colour pattern with size. a, 358 mm DW (SUML BRU112); b, 381 mm DW (SUML BRU113); c, 402 mm DW (SUML BRU035); d, 445 mm DW (SUML JPAG218); e, 447 mm DW (SUML JPAG035); f, 462 mm DW (SUML BRU034); g, 473 mm DW (SUML BRU111); h, c.1000 mm DW. a-g: Philippines; photos and measurements by P. Last; h: Sandakan, Sabah, Malaysia; specimen not saved.

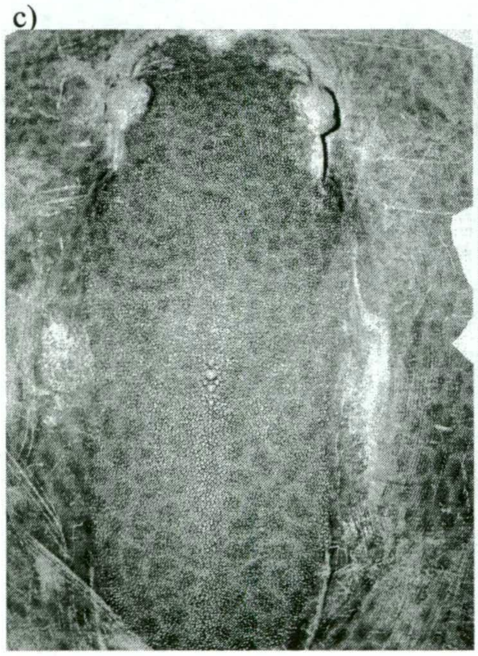
a)



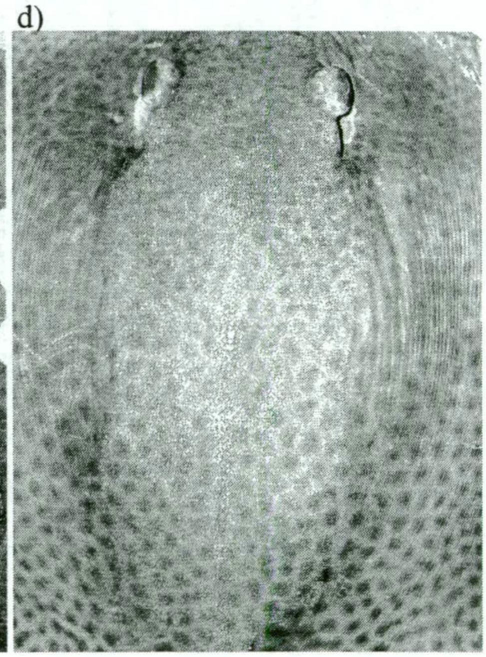
b)



c)



d)



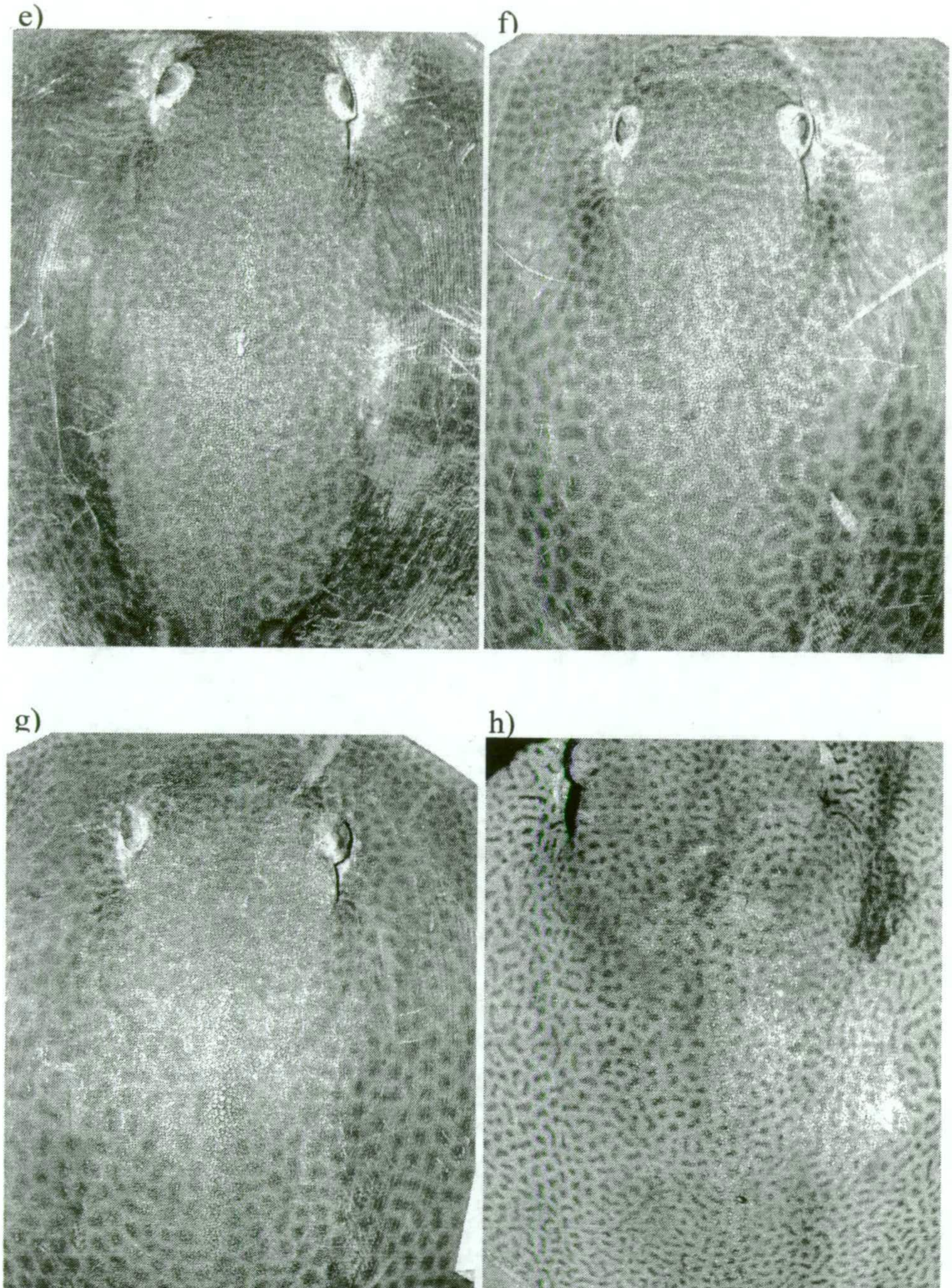

e)
f)
g)
h)

Figure 5.2.15. Representative specimens of *Himantura uarnak* indicating colour variation of large adults in dorsal view. a, 450 mm DW (Irian Jaya, Indonesia; photo by P. Kailola); b, 1400 mm DW (Sandakan, Sabah, Malaysia). Both specimens not saved. Bars 10 cm.

a)

b)

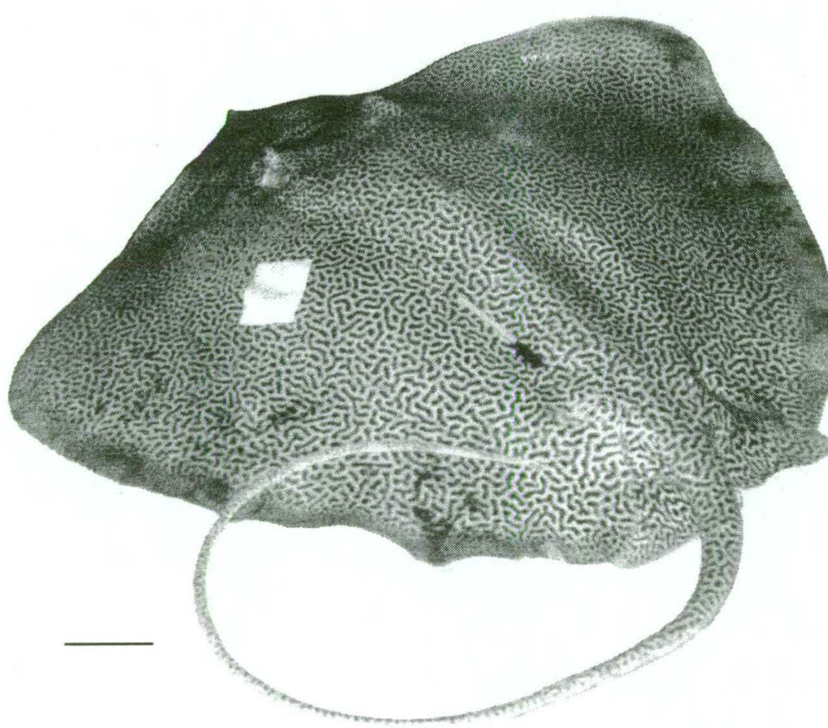
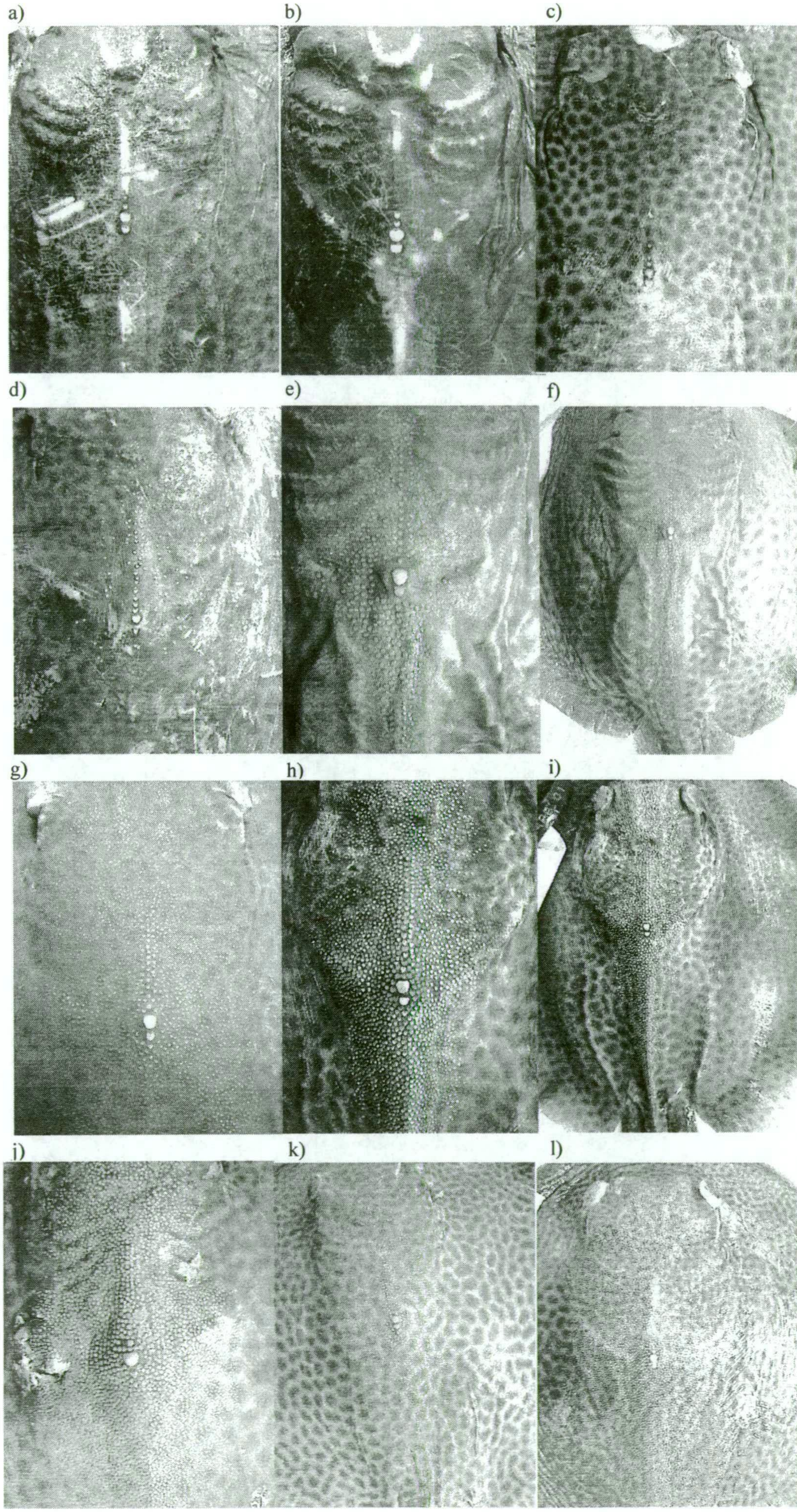


Figure 5.2.16. Representative specimens of *Himantura uarnak* indicating development in squamation (note squamation loosely associated with size) and intraspecific colour variation. a, 270 mm DW (CSIRO H4130.01; male; Manila market, Philippines); b, 275 mm DW (CSIRO H5617.01; female; Semporna, Sabah, Malaysia); c, 273 mm DW (CSIRO H5477.01; male; Kota Kinabalu, Sabah, Malaysia); d, 309 mm DW (CSIRO H5484.01; male; Semporna, Sabah, Malaysia); e-f, 290 mm DW (CSIRO H2371.02; female; Northwest Shelf, Western Australia, Australia); g, 320 mm DW (CAS 213281; female; Thailand); h-i, 310 mm DW (CSIRO H4422.01; male; Repulse Bay, QLD, Australia); j, 325 mm DW (CSIRO H4786.02; male; Lee Point, NT, Australia); k, 300 mm DW (CSIRO H4542.06; male; Kamora estuary, Irian Jaya); l, 373 mm DW (CSIRO H5482.01; male; Tawau, Sabah, Malaysia).


a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)

One or two elongate stinging spine, usually one present.

Meristics. — Total pectoral-fin radials 145-154 (n=11); propterygium 57-64, mesopterygium 18-22, metapterygium 65-72; pelvic-fin radials 25-32 (n=11); vertebral segments 119-124 (n=6), monospondylous 50-55 (n=10), prespine diplospondylous 65-74 (n=5) and postspine diplospondylous 0 (n=11).

Colour. — In fresh, disc diffuse with fine dark brown polygonal spots in young, and with broad dark brown reticulations, and/or short, narrow irregular bars in adults. Spots distributed over light brown background, and bars or reticulations separated by narrow yellowish lines. Ventral disc surface pale, sometimes with moderately wide brownish margin; margin beginning just anterior to oronasal, continuing on to pelvics. Tails of young with a row of dark brown spots on each dorsolateral surface from tail base to sting base; behind sting, tail banded on dorsal and lateral surfaces, with alternating dark and pale bands; dark and pale bands of equal width; uniformly pale on ventral half from tail base to just in front of sting base. Larger specimens and adults, tail with fine dark brown reticulations on a pale (whitish) background, usually becoming blackish towards tail tip, posterior sting.

Skeletal morphology. — Neurocranium of 940 mm DW mature male (Figs. 3.2.7t, 3.2.8s) with relatively short nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval, internasal moderately broad; fontanelle triangular-shaped, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen anteroventral optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate and relatively slender, basally triangular and posteriorly bluntly pointed; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commisure relatively narrow.

Scapulocoracoid unknown.

Pelvic girdle (figure not shown) broadly arched, relatively thin, median prepelvic process absent, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium (Fig. 3.2.12j) relatively simple; 3 basal segments; beta cartilage present as a separate element, merging posteriorly with axial cartilage; dorsal marginal cartilage broad, paddle-shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, subrectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of mixopterygial tip, and broadly extending to lateral surfaces.

Size. — Birth size around 260 mm DW; length at first maturity (males) between 800 and 900 mm DW. A 845 mm DW male specimen observed in the field was determined as being mature (early maturity stage 4), while a larger male with 915 mm DW, as adolescent (late maturity stage 3). A female (CSIRO H1134.3) about 910 mm DW, caught from waters off the North-West Shelf in Western Australia, has two pups (newborns saved as CSIRO H1134.1 and CSIRO H1134.2).

Etymology. — Not specified. However, Rob Kelly (pers. comm. 2000) who helped translate the Latin text into English, noted that *uarnak* is not a Latin word, but suggested that it is probably a place name.

Common name. — Reticulate whipray (Last & Stevens 1994).

Distribution. — Red Sea, India (Bengal Bay), Taiwan, Australia, Papua New Guinea (e.g. Forsskål 1775; McClelland 1841; Blyth 1860; Whitley 1940; Chen & Chung 1971; Myers 1989; Taniuchi *et.al.* 1991).

Comparisons. — *Himantura uarnak* is closest to *H. undulata* (Bleeker), and *H.* sp. A (this study), all three with dorsal disc colour patterning (spots or reticulations), similar in overall disc shape. The spots are smaller, and distance between them closer compared with the other two.

Ontogenetic changes in disc shape most apparent in this species; pectoral fins moderately angular in young, obtusely angular in adults; snout broadest among the three, angle 115-128^{o}.

The rate of squamation in this species is relatively faster compared with the other two closely related species. Newborns are either totally smooth on the back, or with only 1-2 embryonic suprascapular denticles, and specimens with size about 500 mm DW are already covered with a well-developed denticle band along the trunk.

Remarks. — *Himantura uarnak* is the type species of the genus *Himantura*, a species described from the Red Sea. According to Nielsen (1993), Forsskål's specimens of species (including *H. uarnak*) described from the Red Sea were collected during the Arabian Expedition, more than 100 years before the opening (to navigation) of the Suez Canal (the canal was opened in 1869, and construction work began only 10 years earlier, in 1859).

Forsskål's (1775) brief description of the species (number of specimen from which the species was described not specified) is herein reproduced, as based on my interpretation of R. Kelly's (pers. comm.) translation of the original Latin text, i.e. on page viii, 'tail without skin fold', and on page 18, 'similar in description, but completely covered with spots, one sting or two on the tail, which doesn't have any skin fold.'

Apparently, Forsskål's statement 'similar in description' refers to the preceding species, also a new species. Unfortunately, the page with the heading indicating which preceding species, is not available. Due to hindsight, only the relevant pages containing 'uarnak' headings were requested when the article was first requested through the university's interlibrary services; a subsequent attempt to obtain this, and other relevant pages was unsuccessful. It is very likely however, the preceding species referred to is '*Raja sephen pterouros*', following the sequence number on page viii of Forsskåls text; according to R. Kelly (pers. comm.) 'pterouros' is a Greek word, meaning 'wing', which Forsskål may have referred to as the broad skin fold on the tail.

Himantura uarnak is the most frequently quoted species among the *Himantura*'s. It is also noted however, that misidentification of the species is almost as frequent, being most commonly misidentified as one of the other patterned stingrays with banded tail, e.g. *H. toshi* as *H. uarnak* (Gloerfelt-Tarp & Kailola 1984), and *H.* sp. A (this study) as *H. uarnak* (Compagno 1986). On the other hand, Compagno and Heemstra (1984) believed that reports of *H. fava* from southern Africa are erroneous, and suggested these should instead be *H. uarnak.* It is noted herein that *H. fava* (Annandale) is synonymized with *H. undulata* (Bleeker) (this study).

Two original species descriptions, *T. variegatus* McClelland, and *T. (H.) punctata* Günther are proposed as new senior synonyms. In the former, the illustration in the original description, of the large mature male indicates a reticulate disc pattern, and clearly showed a single enlarged midscapular denticle, similar to that described herein. As for the latter, the holotype as examined and photographed by P. Last (pers. comm.), clearly showed it is a juvenile form of *H. uarnak.*

Another species, *T. maculata* Kuhl and van Hasselt, is considered a *nomen nudum*, as it only appeared as a name in Bleeker's (1852) synonymy of *T. uarnak* (see also Eschmeyer On-Line ver. February 15, 2002).

Many of the older works which quoted '*uarnak*', or which synonymized a species with '*uarnak*', particularly those published during the 1700's and 1800's could not be verified within the timeframe of the present study as these papers were not accessed. Some of these works are quoted by such workers as Fowler (1941, quoted: *Raja uarnak* [Gmelin 1789], *R. tafara* Walbaum 1792, *Raia uarnac* Cuvier 1817), and Eschmeyer (quoted: *R. uarnata* Walbaum 1792, *Raia trygononatus longicaudatus* Blainville 1816). It is doubted however, whether the information in those papers will sufficiently help determine the status of each of those listed species; as is usually the case, species are only very briefly described, and remains ambiguous even when illustrations are included.

Much of the confusion regarding identification of *H. uarnak* are apparently due to assumptions that the species is able to change its colour pattern according to the substrate, or that the colour pattern remain the same throughout its life stages, as exemplified earlier. Both these assumptions however, are incorrect, and it is now known that the species undergo ontogenetic transformation of colour patterns during its life stages. Nevertheless, based on available information, there appears to be sub-regional disc colour and disc colour patterns, i.e. northern Australia - New Guinea sub-region forms have larger polygonal spots that are generally dark green (Figs. 5.2.15a, 5.2.16h-k) compared to those from Borneo-Philippines sub-region. Molecular data of some of the Australian - New Guinea form, i.e. DNA analysis of the 16S and cytochrome *b* genes, resulted in representatives of the form clustering among *H. uarnak* (this study; Chapter 4). Another rarer colour form that have been observed is the 'reverse' form, where short irregular pale (whitish) bars are separated by narrow dark brownish lines. Additional specimens are required to determine differences other than colouration.

The transformation of colour pattern, i.e. from spots to reticulations, and from reticulations to bars, is shown herein for the first time (Fig. 5.2.14). The size range in which the spots transform into reticulations is relatively narrow and overlapping, apparently between 350 and 450 mm DW, when the denticle band is well developed. During the transformation stages, reticulations are more apparent along midtrunk, and on the outer and posterior margins of the spiracles, while the edge of disc remain spotted or only sparsely reticulated.

On the other hand, the size range in which reticulations transform into short irregular bars remains unclear, although is appears to be more gradual, but may be widely overlapping as well. Specimens with disc width around 1000 mm are frequently observed having their dorsal disc with short irregular bars, whilst even larger specimens (exceeding 1000 mm DW), are sometimes observed having finely spotted discs, as illustrated by Rüppell (1835; see also Sawyer 1952).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

BMNH 1953.8.10.15[c] (holotype of *Trygon punctata*) ('East Indian Archipelago'); CAS 213281 (Thailand); CSIRO CA715 (Torres Strait, QLD, Australia); CSIRO H322.1 (Papua New Guinea); CSIRO H1134.1, CSIRO H1134.2, CSIRO H1134.3, CSIRO H1463.3, CSIRO H1920.1, CSIRO H1920.2, CSIRO H1920.3, CSIRO H1920.4, CSIRO H2371.02, CSIRO H2371.03, CSIRO H2371.04, CSIRO H2371.05, CSIRO H4016.01 (WA, Australia); CSIRO H4130.01 (Manila, Philippines); CSIRO H4422.01, CSIRO H4786.01, CSIRO H4786.02, NTM S.11144.001, NTM S.11507.006, NTM S.14869.001[c,e] (G of Carpentaria, QLD, Australia); CSIRO H4542.06 (Kamora Estuary, Irian Jaya, Indonesia); CSIRO H5476.03[b,c,e], CSIRO H5477.01[e], CSIRO H5477.02 (Kota Kinabalu, Sabah, Malaysia); CSIRO H5482.01[e] (Tawau, Sabah, Malaysia); CSIRO H5484.01[e], CSIRO H5617.01 (Semporna, Sabah, Malaysia); RMNH 2459[c] (New Guinea);
SMKK KPU5-9196[c] (Kuala Penyu, Sabah, Malaysia); SUML BRU034[c], SUML BRU035[c], SUML BRU111[c], SUML BRU112[c], SUML BRU113[c], SUML BRU114[c], SUML BRU115[c], SUML JPAG035[c], SUML JPAG036[c], SUML JPAG218[c] (Palawan, Philippines).

Himantura undulata (Bleeker 1852)

Bleekers variegated whipray

Figures 3.2.5q, 3.2.6p, 3.2.7u, 3.2.8t, 3.2.9i, 3.2.10q, 3.2.11p, 3.2.12k, 5.2.17–5.2.21; Tables 5.2.11–5.2.12

Trygon undulata Bleeker 1852: 70 (original description based on 3 specimens, including one male, 270-320 mm disc width, not figured). Two possible syntypes: BMNH 1867.11.28.156, 264 mm disc width, female; RMNH 7440, 320 mm disc width, female (measurements by P. Last). Type localities: Batavia (=Java) and Samarang (=Semarang), both in Indonesia.

Synonymy. —

Trygon russellii (not Gray): Blyth 1860, 42 (description, misidentification in part). Locality: Lower Bengal.

Trygon (Himantura) undulatus: Duméril 1865, 586 (?description). Locality: Malabar.

Leiobatis (Himantura) undulatus: Bleeker 1877, figs. a and b, pl. 562, Plagiostom. Pl. 40 (illustration of unidentified male syntype).

Trygon favus Annandale 1909: 25, fig. 3 (pl. I), fig. 10 (pl. III) (description based on two specimens, one 1300 mm disc width, both females, photographed, including an illustration of the oral papillae, mouths of both specimens and skin of the back of one of the specimens saved in the Indian Museum as registration number ZSI F2411/1). Type locality: Bay of Bengal, off coast of Orissa, India; October 1908; caught by trawling aboard the 'Golden Crown'.

Dasybatus (Himanturus) favus: Garman 1913, 377 (description after Annandale).

Dasyatis (Himantura) favus: Fowler 1941, 412 (description after Annandale).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape suboval, preorbital snout moderately long, with a distinct apical lobe, lateral apices moderately rounded. Orbits small, slightly protruded. Dorsal surface entirely covered with large dark brown polygonal spots in young, and with broad yellowish-brownish undulations and elongated loops, or large and hollow polygonal spots in larger specimens and in adults; spots or loops separated by slightly narrower or equally wide paler (white) lines. Tails of young banded on dorsal and lateral surfaces (dark bands almost 3 times wider pale bands); larger specimens and adults, tail with fine dark brown reticulations on a pale (whitish) background. Three midscapular denticles, always arranged in a row, the anteriormost pearl-shaped, and largest among the three; the second and third slightly smaller, broad and narrow heart-shaped respectively.

Description. — Disc suboval, width 0.98-1.00 times length; robust, center raised at mid-scapular, maximum disc thickness 0.11-0.12 in disc width (DW); preorbital snout moderately long, with a distinct apical lobe, angle 109-110.5^{o}; anterior margins of disc strongly concave, lateral apices moderately rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.17-5.2.21). Pelvic fins moderately long, 19.1-19.8% DW; width across base 12.3-13.6% DW. Claspers of adult male (Fig. 3.2.5q) long and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, weak notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length about 3 times disc width (tail cut in all specimens examined); base narrow, subcircular in cross-section, width 1.32-1.39 times height at base.

Snout moderately long, depressed; preoral snout length 3.57-3.83 times mouth width, 2.83-2.96 times internarial distance, 29.5-30.5% DW; direct preorbital snout length 1.87-2.13 times interorbital length, horizontal length 1.80-2.01 times interorbital length; snout to maximum disc width 44.8-46.3% DW; interorbital space flat; eye moderately large, diameter 48-55% spiracle length; orbits slightly protruded, diameter 0.67-0.72 in spiracle length, interorbital distance 2.70-3.07 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak double concavity, length 0.42-0.46 in internasal distance; internasal distance 0.44-0.45 of prenasal length, 2.17-2.36 times nostril length. Nasal curtain skirt-shaped, relatively broad, width 2.06-2.08 times length; lateral margin weakly double concave, smooth edged;

posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth slightly arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw papillose, not confined to narrow strip around lips. Mouth floor with 2 broad-based papillae, distally pointed (subtriangle), connected medially by a low serrated ridge; four papillae in tentative syntype specimen (P. Last, pers. comm.).

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth row counts not available.

Gill opening margins smooth, straight; length of first gill slit 1.28-1.47 times length of fifth, 0.37-0.41 of mouth width; distance between first gill slits 1.93-2.03 times internasal distance, 0.39-0.40 of ventral head length; distance between fifth gill slits 1.19-1.31 times internasal distance, 0.23-0.25 in ventral head length.

Squamation. — Stages of squamation with narrow size ranges, stages simultaneously developing with multiple overlap. Denticles with stellate bases present in all the non-type specimens examined. (According to Annandale [1909], these are absent in the large holotype of *H. fava*. However, it is more likely that the stellate-based denticles are minute, that these are not easily observed in large specimen).

Syntypes in early part of Stage 4 (Fig. 5.2.17): dorsal surface with a regular longitudinal secondary denticle band along the trunk, beginning interorbital to tail base at pectoral-fin insertion; band subrectangular, width confined to interspiracular width, anteriorly extending to just in front of orbits, slightly constricted just after scapular, margin well-defined; Denticles flat, heart-shaped, sparse, uniformly widely-spaced (i.e. about 1-1½ denticle length apart); large pearl-shaped suprascapular denticle (one to two) present (length of largest 4.9-5.2 mm). Tail void of denticles.

Stages 0 and 4: from birth (ca. 260 mm DW) — Dorsal surface of disc with a longitudinal secondary denticle band along the trunk, beginning interorbital to tail base; and a large pearl-shaped suprascapular denticle. Denticles blunt conical, sparse, uniformly widely-spaced.

During late part of these stages (ca. 310 mm DW), secondary band narrowly extends to a point just after level of pectoral-fin insertion; a second suprascapular denticle, followed by a third one appearing behind the first; broad and narrow heart-shaped respectively. Size of largest suprascapular denticle range between 4.9 and 5.2 mm (n=3).

Stages 1, 3 and 4: (ca. 350 mm DW) — Primary, median denticle band within the existing secondary denticle band becoming conspicuous, seemingly simultaneous with the development of independent row(s) of enlarged denticles along midline of the tail. Enlarged denticles (squamation Stage 3) more conspicuous in some; narrow heart-shaped with its posterior tip extended and pointed (i.e. hook-like in lateral view) (Fig. 5.2.19; see also remarks).

Secondary band remain subrectangular, width slightly expanded above nape, narrowing gradually posteriorly to anterior of pectoral-fin insertion, terminating in 2-3 rows consisting of a few denticles; margin well-defined. Tail with weak evidence of denticles on lateral surfaces just anterior to stings, increasing dorsally from behind sting to tail tip; denticles along tail almost uniform in size, progressively becoming smaller nearer tail tip; ventrally, from tail base to tip of sting, denticles lacking (naked).

Denticles in primary band with slightly convex crown, heart-shaped, almost twice as large as those in secondary band; closely-set, not imbricated. Denticles in secondary band flat, heart-shaped, and interspersed with smaller, stellate-based conical denticles; closely-set, not imbricated, those near the band margin more widely-spaced between each other.

As the development progresses (>430 mm DW), primary band becomes inconspicuous; more denticles appearing in the secondary band. Denticles also appear on the snout (concentrating at tip), and on the outer spiracular margin; denticles minute, stellate-based conical; more conspicuous to the naked eye in very large specimens (i.e. CSIRO H5481.01; 980 mm DW). Distance between denticles in the bands including the three suprascapular denticles increasing (Fig. 5.2.21).

Stages 5 and 6 not applicable for this species.

Single elongate stinging spine.

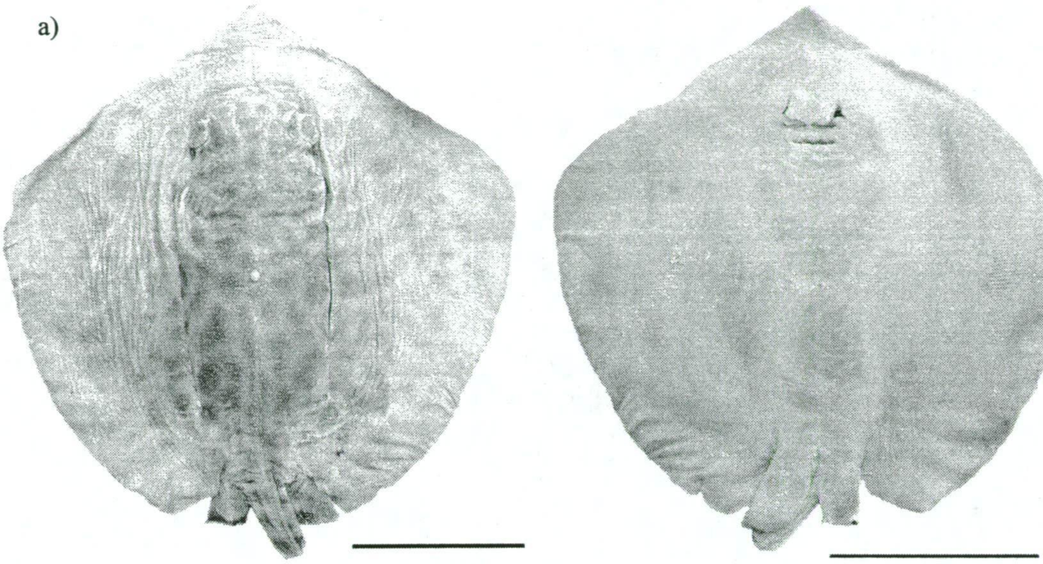
Meristics. — Total pectoral-fin radials 149-154 (n=3); propterygium 62-63, mesopterygium 21-25, metapterygium 65-69; pelvic-fin radials 24-28 (n=3); vertebral segments 112 (n=1), monospondylous 46-49 (n=3), prespine diplospondylous 63 (n=1) and postspine diplospondylous 0 (n=1).

Colour. — In fresh, entire disc diffuse with large dark brown polygonal spots in young, and with broad yellowish-brownish undulations and elongated loops, or large and hollow polygonal spots in larger specimens and in adults; spots or loops separated by slightly narrower or equally wide paler (white) lines. Ventral disc surface pale, usually with moderately wide brownish margin; margin beginning just anterior to oronasal, continuing on to pelvics. Tails of young appear banded on dorsal and lateral surfaces, with alternating dark and pale bands behind sting; ventral surface uniform pale. Dark bands almost 3 times wider pale bands. Larger specimens and adults, tail with fine dark brown reticulations on a pale (whitish) background.

It appears that dorsal disc colour pattern may be sexually dimorphic (Fig. 5.2.20), based on the limited number of materials available at hand.

Figure 5.2.17. Two possible female syntypes of *Himantura undulata*. a, BMNH 1867.11.28.156 (264 mm DW; female; 'East Indies') in dorsal and ventral view; b, RMNH 7440 (310 mm DW; female; locality unknown) in dorsal view. Photos and measurements by P. Last. Bars 10 cm.

a)



b)

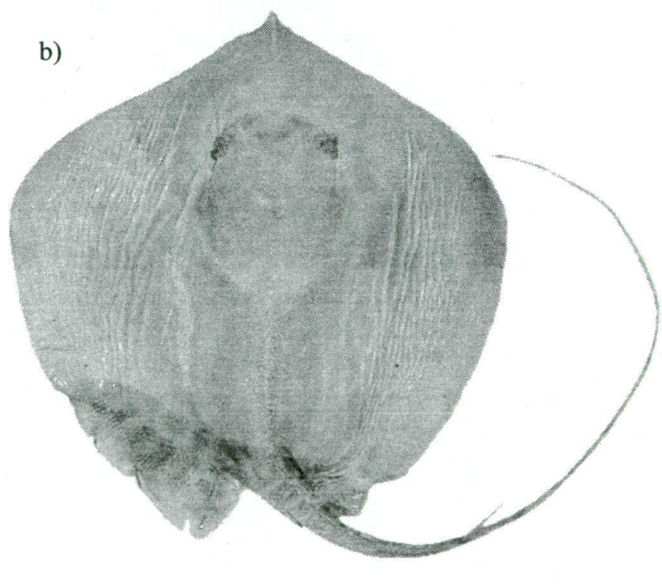


Figure 5.2.18. Illustration of *Himantura undulata* (reproduced from Bleeker 1877: fig. a, pl. 562, Plagiostom. Pl. 40).

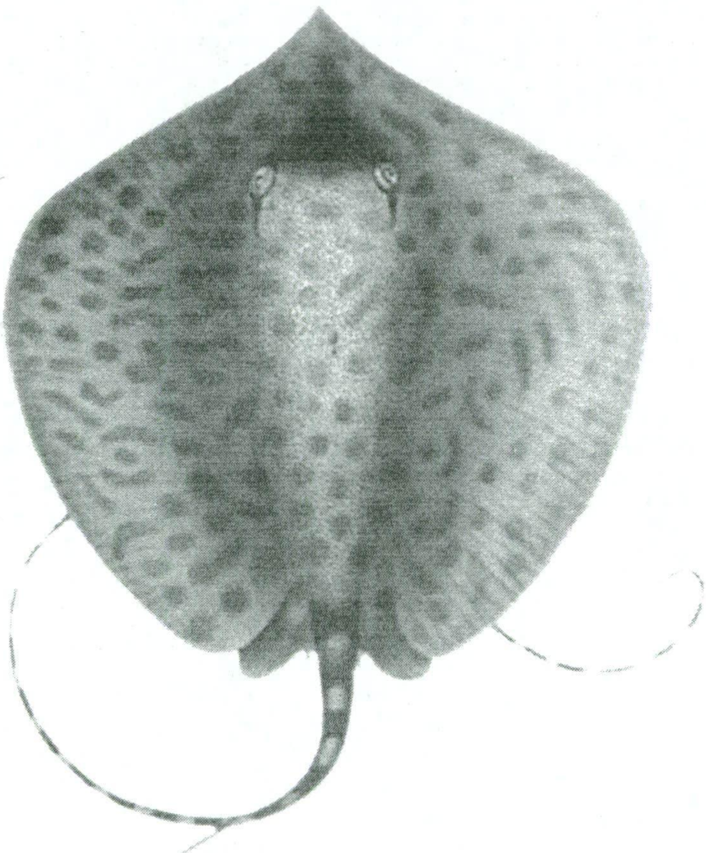


Figure 5.2.19. Representative specimen of *Himantura undulata* in dorsal and ventral views (a-b); c, tail base in dorsal and lateral views (note hooked or backward-curving row of enlarged denticles). CSIRO H5482.02 (360 mm DW; female; Tawau, Sabah, Malaysia). Photos by T. Carter. Bars 10 cm.

a)

b)

c)

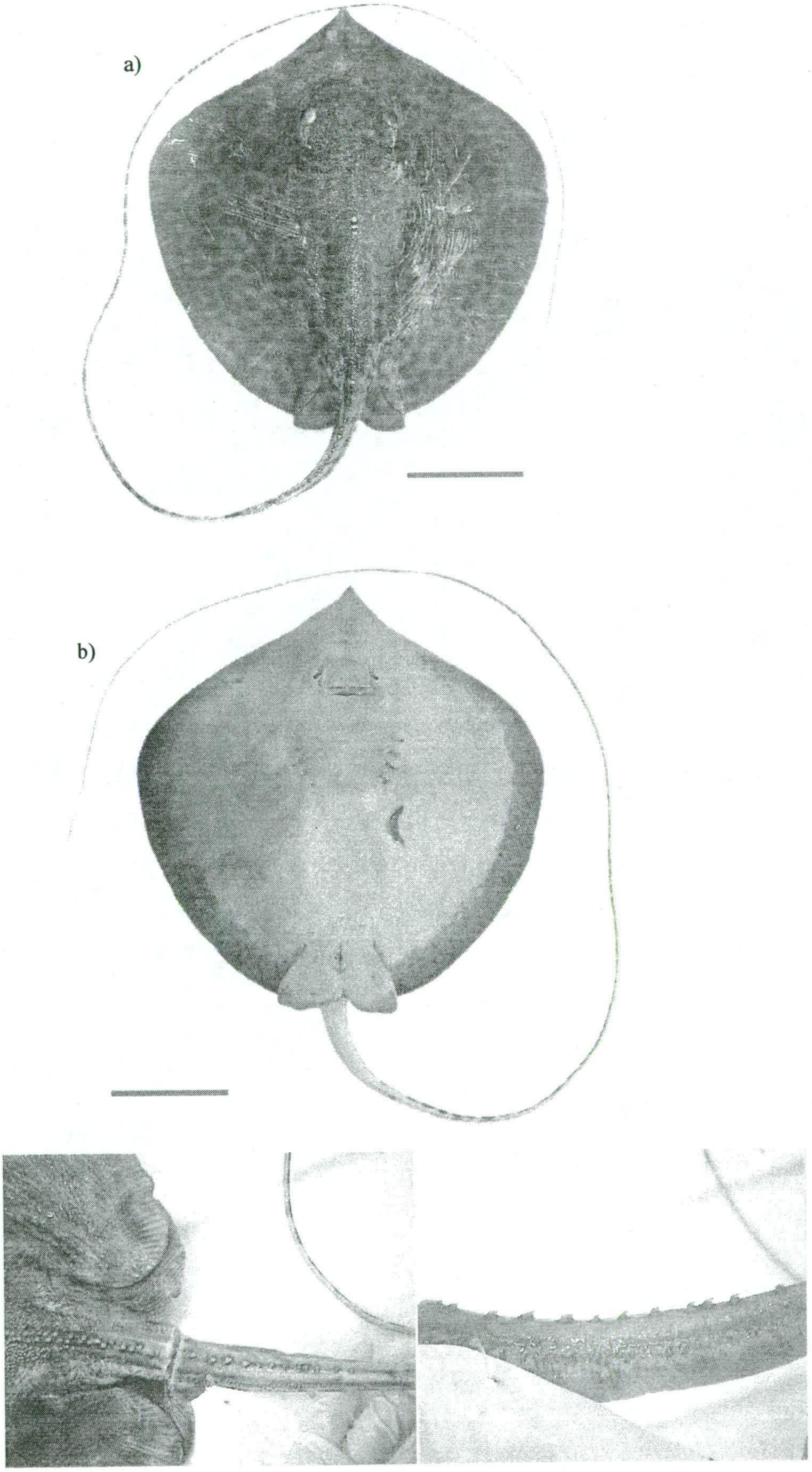


Figure 5.2.20. Representative specimens of *Himantura undulata* indicating transitional colour pattern with size. a, 264 mm DW (BMNH 1867.11.28.156; female); b, 644 mm DW (specimen not saved); c, 840 mm DW (specimen not saved); d, 891 mm DW (specimen not saved; mature male); e, 980 mm DW (some parts saved as CSIRO H5481.01; mature male); f, 1300 mm DW (holotype of *Trygon favus* Annandale 1909; female; Bay of Bengal, off coast of Orissa, India; reproduced from Annandale 1909: 25). a: 'East Indies'; b-c, e: Sandakan, Sabah, Malaysia; d: Indonesia. a, d: photos and measurements by P. Last. Bar 10 cm.

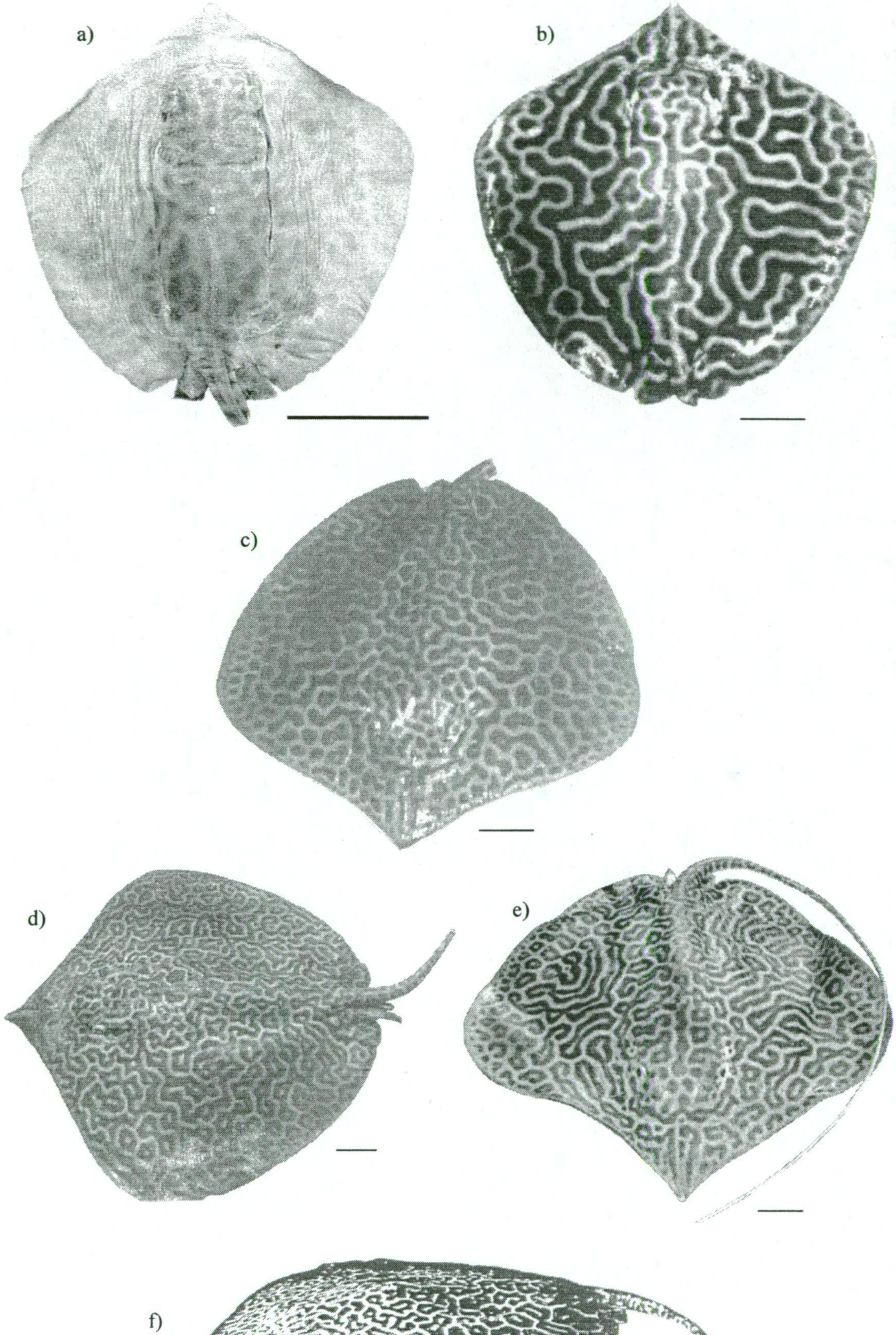
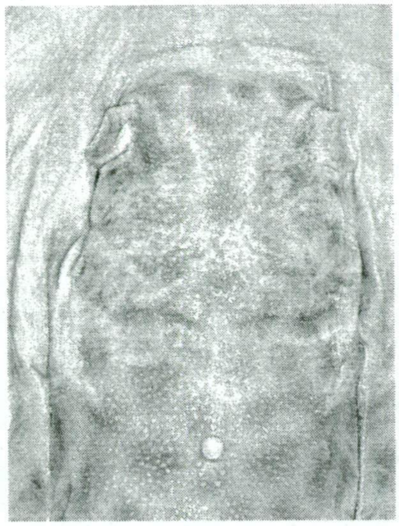
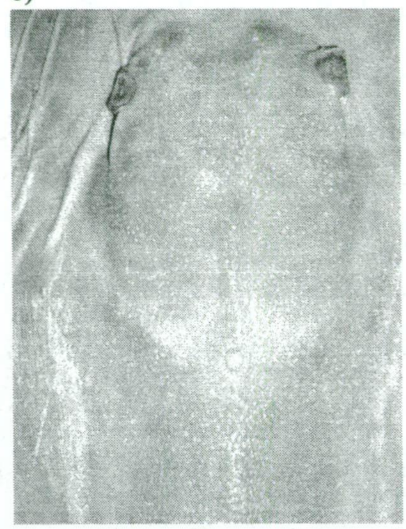

a)
b)
c)
d)
e)
f)

Figure 5.2.21. Representative specimens of *Himantura undulata* indicating squamation. a, 264 mm DW (BMNH 1867.11.28.156; female; 'East Indies'; photos and measurements by P. Last); b, 310 mm DW (RMNH 7440; female; locality unknown); c, 360 mm DW (CSIRO H5482.02; female; Tawau, Sabah, Malaysia); d, 430 mm DW (CSIRO H5483.01; immature male; Sipitang, Sabah, Malaysia); e, 980 mm DW (CSIRO H5481.01, parts only; mature male; Sandakan, Sabah, Malaysia).

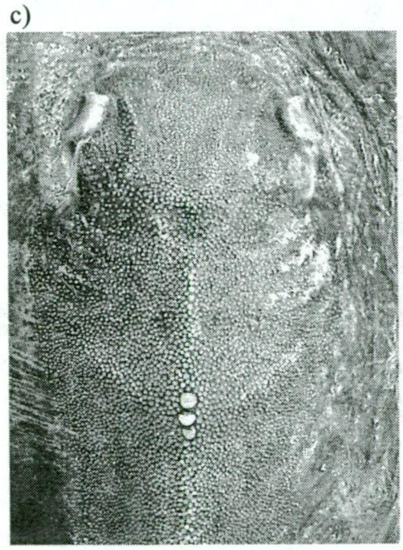
a)



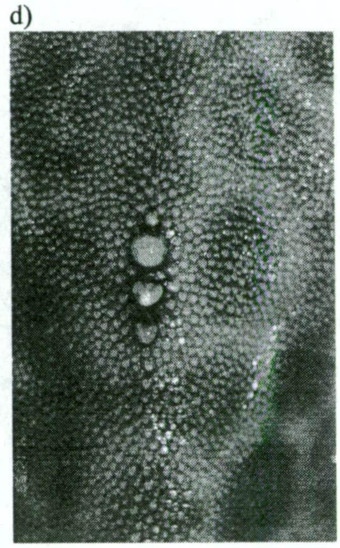
b)



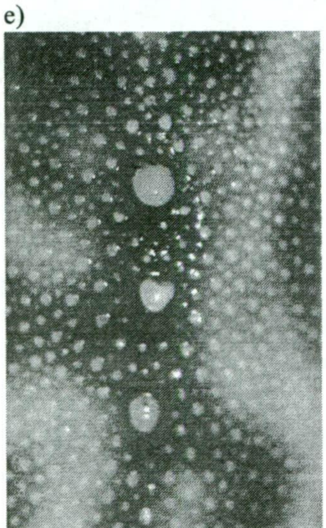
c)



d)



e)



Skeletal morphology. — Neurocranium of 980 mm DW mature male (Figs. 3.2.7u, 3.2.8t) with moderately elongate nasal capsules; anterior edge broadly angular, broadly concave medially; nasal apertures transversely oval, internasal broad; fontanelle triangular-shaped, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen anterior optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate and robust, basally triangular and posteriorly bluntly pointed; supraorbital crests low and strong, slightly concave along orbital margin; sphenopterotic ridge a narrow ledge with two small pointed processes; lateral commisure broad.

Scapulocoracoid (Fig. 3.2.10q) relatively broad, moderately high, posterior part strongly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to narrow articular condyle at tip of scapular process; two small postdorsal foramina; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle moderately high, 2.5-3 times as high as long; mesocondyle long and narrow, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11p) moderately arched, relatively thick, median prepelvic process absent, small anterolateral processes, moderately long dorsal iliac processes, and narrowly rounded mesial ischial processes.

Mixopterygium (Fig. 3.2.12k) relatively simple; 2 basal segments; beta cartilage present as a separate element, merging posteriorly with axial cartilage; dorsal marginal cartilage broad, paddle-shaped, posterior edge merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, suboval rectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of mixopterygial tip, and narrowly extending to lateral surfaces.

Size. — Birth size around 260-270 mm DW; length at first maturity (males) between 600 and 700 mm DW. A 456 mm DW male specimen (CSIRO H5482.03) was determined as being an immature (maturity stage 2), while a male specimen (specimen not saved; Fig. 5.2.20d, courtesy of P. Last) 891 mm DW, as mature (maturity stage 4). The largest male specimen observed is 980 mm DW (Fig. 5.2.20e, only partly saved; CSIRO H5481.01), from Sandakan (Sabah, Malaysia). Females reaching to 1300 mm DW, as reported by Annandale (1909) of the holotype of *Trygon favus*.

Etymology. — Not specified, but Bleeker implied the name as based on the patterns on the dorsal surface of the disc (i.e. broad undulating stripes, and large polymorphic spots).

Common name. — Bleekers variegated whipray.

Distribution. — Indonesia (Java; Semarang), Australia, Malaysia, India (Lower Bengal; Orissa) (e.g. Bleeker 1852; Blyth 1860; Annandale 1909; Last & Stevens 1994).

Comparisons. — *Himantura undulata* is closest to *H. uarnak* Forsskål, and *H.* sp. A (this study), all three with dorsal disc colour patterning (spots or reticulations), similar in overall disc shape. This species is particularly unique in its squamation (arrangement of the midscapular denticles), and shape of the oral papillae.

In *H. undulata*, the young are born with large dark brown polygonal spots, and a developed secondary denticle band. The young of *Himantura* sp. A are also born with polygonal spots, although smaller in size, and are naked (void of denticles), whilst in *H. uarnak*, the dorsal surface of the discs of newborns and young are covered small round spots, and are naked. The midscapular denticles among the three species are unique; in *H. undulata*, three midscapular denticles are present, the anteriormost pearl-shaped, the second and third, broad and narrow heart-shaped respectively, and are slightly smaller in size compared to the first one.

The oral papillae in *H. undulata* is ridge-shaped, i.e. two bluntly triangular processes with irregularly serrated margins joined together by a similarly serrated ridge, and is rather flap-like. The oral papillae in the other two consist of long finger-like projections.

Differences in disc shape among the three lies in the shape of the anterior part of the disc, i.e. in *H. undulata*, the anterior margins of disc are strongly concave, and lateral apices moderately rounded, whereas in *H. uarnak*, the anterior margins of disc are weakly concave, and lateral apices of the disc moderately angular, and in *H.* sp. A, the anterior margins of disc are double convex, and lateral apices moderately angular to narrowly rounded.

Remarks. — Bleeker described *Trygon undulata* based on three syntypes from Jakarta and Semarang, whose sizes range between 270-320 mm DW. The species, illustrated later in his Atlas Ichthyologique (Bleeker 1877), depicts an immature male specimen with an intact tail and a single elongate sting, and is presumably the single immature male syntype he described years earlier. Bleeker (1852, 1877) neither listed nor mentioned of any catalogued specimens, although two syntypes are listed by Eschmeyer (On-Line ver. February 15, 2002). Eschmeyer also noted that *T. undulata* appeared first as name only in a list by Bleeker dated 1850. Both these putative types were examined (details below), and found to be the young form of another species identified as *Himantura fava* (Annandale 1909).

Annandale described *Trygon favus* based on two specimens, and designated one of them, a large female 1300 mm DW, caught from the Bay of Bengal off Orissa coast in India, as the holotype (Anandale's figure of the holotype reproduced in Fig. 5.2.20f). He noted that only the mouth and some parts of the dorsal skin of the holotype were saved, and gave the registration number ZSI F2411/1 for the parts now in the Indian Museum. Attempts were not made to access the materials during this study however, mainly due to the fact that a previous visit there failed to locate the specimen (P. Last pers. comm.).

According to Compagno (pers. comm. 1997), '*H. fava* is bit of a mystery. I've only seen a single specimen, from the Gulf of Thailand. It was described, by I believe, from the Bay of Bengal. Peter Last thinks that it may be a synonym of *H. undulata*, which may be correct...'. Thus, it seems likely this was the specimen referred to in Compagno and Roberts (1982); the meristic data (i.e. 153 total pectoral radials, 115 free vertebral centra; last centrum a short distance anterior to origin of stings) given for this uncatalogued specimen in the California Academy of Sciences collection, would have been more useful for compariosn purposes had the counts for pro-, meso-, and meta- pterygial radial be given instead. It appears he (Compagno) is now not sure about its identity, and that he implicitly stated the holotype of *H. fava* was not examined.

The two putative syntypes of *H. undulata* (i.e. BMNH 1867.11.28.156 and RMNH 7440) listed by Eschmeyer, as examined by P. Last (pers. comm. 2001), are noted to have the label on each specimen without proper labels supporting or indicating their type status. The label on the BMNH specimen indicated 'East Indies' (a name formerly applied to southeastern Asia; nations of East Indies are Cambodia, India, Indonesia, Malaysia, Myanmar, Sri Lanka and Vietnam) as the locality, whilst the label on the RMNH specimen did not specify any locality.

The BMNH specimen, 254 mm DW, has its tail cut off before the sting (Fig. 5.2.17a), whilst the RMNH specimen, about 310 mm DW, has an intact tail and sting (Fig. 5.2.17b). Both these female specimens are relatively small sized, the former smaller (i.e. outside the disc width range given by Bleeker). However, in comparing Bleeker's illustration of the male syntype of *H. undulata* (Fig. 5.2.18) with photographs (courtesy of P. Last) of the two syntypes, all three appear to be conspecifics, and are very similar particularly in disc shape and squamation (shape and orientation of midscapular denticle).

Himantura undulata sensu Last and Stevens (1994), and later sensu Last and Compagno (1999) is non Bleeker. In their species description of *H. undulata* (Bleeker), Last and Compagno synonymized *H. fava* (Annandale) with this species, and noted that the species (*H. undulata*) is 'often confused with *H. uarnak*, and that another colour form with very large rings over the disc (known as *H. fava*) may be a distinct species.'

Although Last and Compagno are correct in placing *H. fava* in the synonymy of *H. undulata*, the illustration (after Last & Stevens) given however, depicts that of an adult form with large irregular rings over the entire disc, and which appear to be the 'distinct species' they referred to. Moreover, the form described and illustrated by Last and Stevens, and by Last and Compagno is different from that described by Bleeker, and is herein recognized as a separate valid species.

Hence, Last and Stevens, and Last and Compagno have wrongly applied the name *H. undulata* to denote a previously undescribed species. Based on the strict provision of the 'Use of species-group names wrongly applied through misidentification Article 49' of the ICZN (1999), the species-group name *undulata* cannot be employed denote the new species. This new species is herein tentatively named *Himantura* sp. A; details are discussed under that species heading. Whereas Bleeker's *H. undulata* is retained, and used to describe the species as intended by Bleeker, while *H. fava* (Annandale) is considered its senior synonym, and consequently sunk.

Another nominal species considered as a senior synonym of Bleeker's *H. undulata*, is *Trygon russellii* sensu Blyth 1860. This species as described by Blyth is non Gray (1834); on the other hand, *T. russellii* Gray is considered as a possible name for *H.* sp. A (see remarks under that species heading).

Trygon russellii sensu Blyth is partly misidentified as *H. undulata*, and partly as *H.* sp. A, and is considered a senior synonym of Bleeker's *H. undulata* based on the following statement, '...tubercles on back sparse and heart-shaped, and a single line of them (prolonged to more or less into backward-curving prickles) is continued along the median line of the tail as far as its (stinging) spine. These are retained in a specimen 12 inches (~30 mm) in length (to base of tail), but in another of the same size, they had disappeared or perhaps had never made their appearance...'.

A similar pattern of squamation was observed in one of the female specimens (360 mm DW) examined (Fig. 5.2.19), but not in another smaller female specimen, or in larger males. Nevertheless, apart from the 'enlarged and backward-curving row of denticles' lacking or inconspicuous, all the materials examined agree in both external and internal characteristics (i.e. morphometric ratios, meristic counts, dorsal disc colour patterns).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CSIRO H5481.01[b,c,e] (Sandakan, Sabah, Malaysia); CSIRO H5482.02[a,e], CSIRO H5482.03 (Tawau, Sabah, Malaysia); CSIRO H5483.01[e] (Sipitang, Sabah, Malaysia); BMNH 1867.11.28.156[c] (possible syntype) (East Indies); RMNH 7440[c] (possible syntype) (unspecified locality); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

Himantura sp. A

Leopard whipray

Figures 3.2.5s, 3.2.7v-w, 3.2.8u-v, 3.2.9k, 3.2.10s, 3.2.11r-s, 5.2.22–5.2.26; Tables 5.2.13–5.2.14

Synonymy. —

?*Trigon russellii* Gray 1834: 100 (?original description, ?illustrated, paper not seen; quoted by Gray 1851). Locality: India.

?*Trygon russelli*: Gray 1834, t. 100 (misspelling of *russellii* Gray, paper not seen; quoted by Gray 1851). Locality: India.

Trygon russellii: Blyth 1860, 42 (description, misidentification in part). Locality: Lower Bengal.

Dasyatis russellii: Fowler 1904, 499 (listed). Locality: Sumatra, Indonesia.

Dasyatis uarnak (not Forsskål): Wallace 1967, 44 (description, morphometrics, illustration of a 707 mm disc width female). Locality: Natal coast.

Himantura fava (not Annandale): Compagno & Roberts 1982, 323, 336 (listed, brief description, distributional limit, misidentification in part).

Himantura sp. 1: Gloerfelt-Tarp & Kailola 1984, 38 (brief description, illustrated, misidentification). Locality: Indonesia (Bali to Sumatra).

Himantura uarnak (not Forsskål): Compagno 1986, 139, fig. 30.10 (brief description, illustrations of specimens with 335 mm and 1200 mm disc width, misidentification in part). Localities: Eastern Cape to Natal and Mozambique.

Himantura uarnak (not Forsskål): Compagno *et al.* 1989, 108 (misdentification in part). Locality: Southeast and East Coast from East London to Natal and Southern Mozambique, South Africa.

Himantura undulata (not Bleeker): Last & Stevens 1994, 408 (description, illustrated). Locality: northern Australia.

Himantura undulata (not Bleeker): Last & Compagno 1999, 1492 (description, illustration after Last & Stevens [1994]). Locality: Indo-West Pacific.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, preorbital snout moderately long, with a distinct apical lobe, lateral apices moderately angular to narrowly rounded. Orbits moderately large, slightly protruded. Dorsal surface entirely covered with moderately large dark brown polygonal spots in young; large (>550 mm DW) specimens with thick dark brown irregular rings (often rings incomplete, and with open ends), each ring yellowish inside - resembling markings (spots) on leopards. Tails of young with spots on each dorsolateral surface from its base to sting base, entirely banded behind the sting, with alternating dark and pale (white) rings; ventral surface from tail base to sting base uniform pale. Primary band developing as a single row of enlarged widely spaced narrow heart-shaped denticles, comprising up to 9 denticles anterior to, and 5 smaller ones posterior to two broad heart-shaped suprascapular denticles.

Description. — Disc rhomboidal, width 1.00-1.16 times length; robust, center raised at mid-scapular, maximum disc thickness 0.10-0.14 in disc width (DW); preorbital snout moderately long, with a distinct apical lobe, angle 101-119.5^{o}; anterior margins of disc double convex, lateral apices moderately angular to narrowly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.2.22-5.2.26). Pelvic fins moderately long, 17.1-19.0% DW; width across base 10.8-13.4% DW. Claspers of adult male (Fig. 3.2.5s) long and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, prominent notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.53-3.77 times disc width; base narrow, subcircular in cross-section, width 1.14-1.31 times height at base.

Snout moderately long, depressed; preoral snout length 2.79-3.30 times mouth width, 2.33-2.69 times internarial distance, 21.5-27.6% DW; direct preorbital snout length 1.25-1.73 times interorbital length, horizontal length 1.12-1.64 times interorbital length; snout to maximum disc width 37.9-38.0% DW; interorbital space slightly convex; eye moderately large, diameter 28-53% spiracle length; orbits slightly protruded, diameter 0.49-0.80 in spiracle length, interorbital distance 2.48-

3.63 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak double concavity, length 0.40-0.47 in internasal distance; internasal distance 0.47-0.56 of prenasal length, 2.11-2.49 times nostril length. Nasal curtain subrectangular, relatively broad, width 1.87-1.92 times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately papillose, not confined to narrow strip around lips. Mouth floor with 4 short papillae; medial pair simple, rounded distally, longitudinally flattened, subequal in size and almost two times larger than outer pair, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth rows 28 in upper jaw; not available for lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.32-1.51 times length of fifth, 0.33-0.44 of mouth width; distance between first gill slits 1.98-2.18 times internasal distance, 0.41-0.45 of ventral head length; distance between fifth gill slits 1.25-1.40 times internasal distance, 0.25-0.28 in ventral head length.

Squamation. — Stages of squamation with narrow size ranges, with Stages 1 and 4 simultaneously developing. Rate of squamation relatively slow, still sparsely covered with denticles at 500 mm DW.

Stage 0: from birth (ca. 200 mm DW) (Figs. 5.2.23a, 5.2.26a) — Disc entirely smooth; a few minute denticles above the first synarcual appearing earlier or later.

Stages 1 and 4: (ca. 330 mm DW) (Fig. 5.2.22) — Denticles above first synarcual and scapular becoming more exposed, forming the primary, median denticle band and suprascapular denticles. Development of primary band seemingly simultaneous with the initial development of a continuous secondary denticle band along the trunk.

Primary band developing as a single row of enlarged widely spaced narrow heart-shaped denticles, comprising up to 9 denticles anterior to, and 5 smaller ones posterior to the two suprascapular denticles; space between each denticle in the row initially wider (2-3 times) than length of each denticle. Suprascapular denticle broad heart-shaped with convex crowns (length 4.6-5.3 mm; n=5).

The secondary denticle band forming a narrow longitudinal shape along the trunk, from interorbital to adjacent the primary band continuing to tail base; band with weakly defined margin. Denticles uniform flat narrow heart-shape, widely spaced with about 1-3 denticles apart, gradually decreasing in size and number towards band margin.

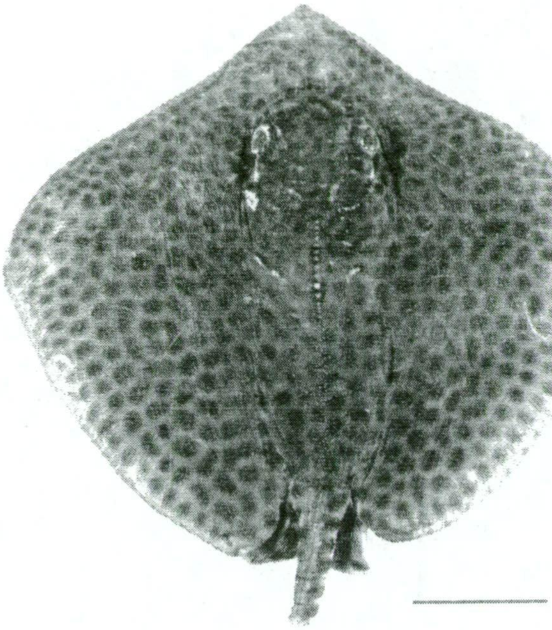
Late stage 4, denticles fully exposed, but continue developing; band forming subrectangular shape along the trunk; anteriorly terminating just in front of orbits, tapering gradually posteriorly to a narrow band at tail base before continuing on to tail; band margin well-defined.

Stages 2, 3, 5 and 6 not applicable for this species.

Single elongate stinging spine in all specimens examined.

Meristics. — Total pectoral-fin radials 152-158 (n=4); propterygium 60-65, mesopterygium 20-23, metapterygium 69-74; pelvic-fin radials 24-31 (n=4); vertebral segments 115-123 (n=5), monospondylous 48-55 (n=5), prespine diplospondylous 62-70 (n=4) and postspine diplospondylous 0 (n=2).

Figure 5.2.22. Representative specimen of typical *Himantura* sp. A in dorsal and ventral views. CSIRO H5478.01 (455 mm DW; female; Kota Kinabalu, Sabah, Malaysia). Photos by T. Carter. Bars 10 cm.



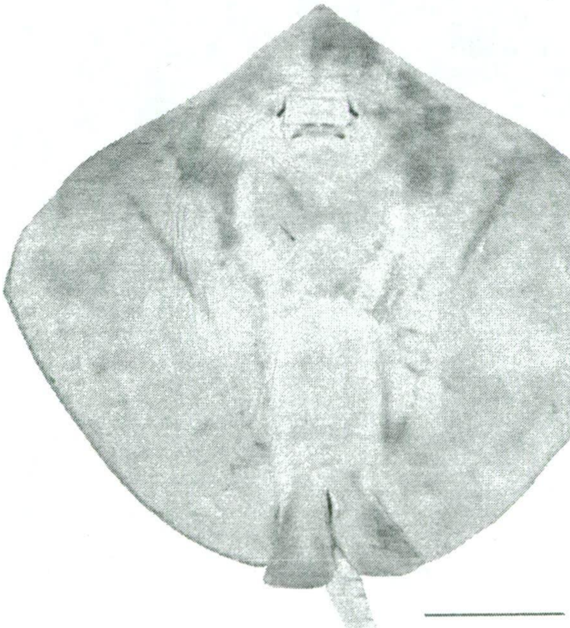


Figure 5.2.23. Representative specimens of typical *Himantura* sp. A indicating transitional colour pattern with size. a, 200 mm DW (CSIRO H635.02; female; Northern Territory, Australia; photo by T. Carter); b, 260 mm DW (NTM S.10765.002; female; Indonesia; photo by P. Last); c, 660 mm DW (UMS MMKK136; female; Kota Kinabalu, Sabah, Malaysia); d, 805 mm DW (CSIRO H5284.05, parts only; female; Kota Kinabalu, Sabah, Malaysia); e, 1105 mm DW (CSIRO H2903.01; female; Gulf of Carpentaria, Australia; photo by T. Carter). Bars 10 cm.

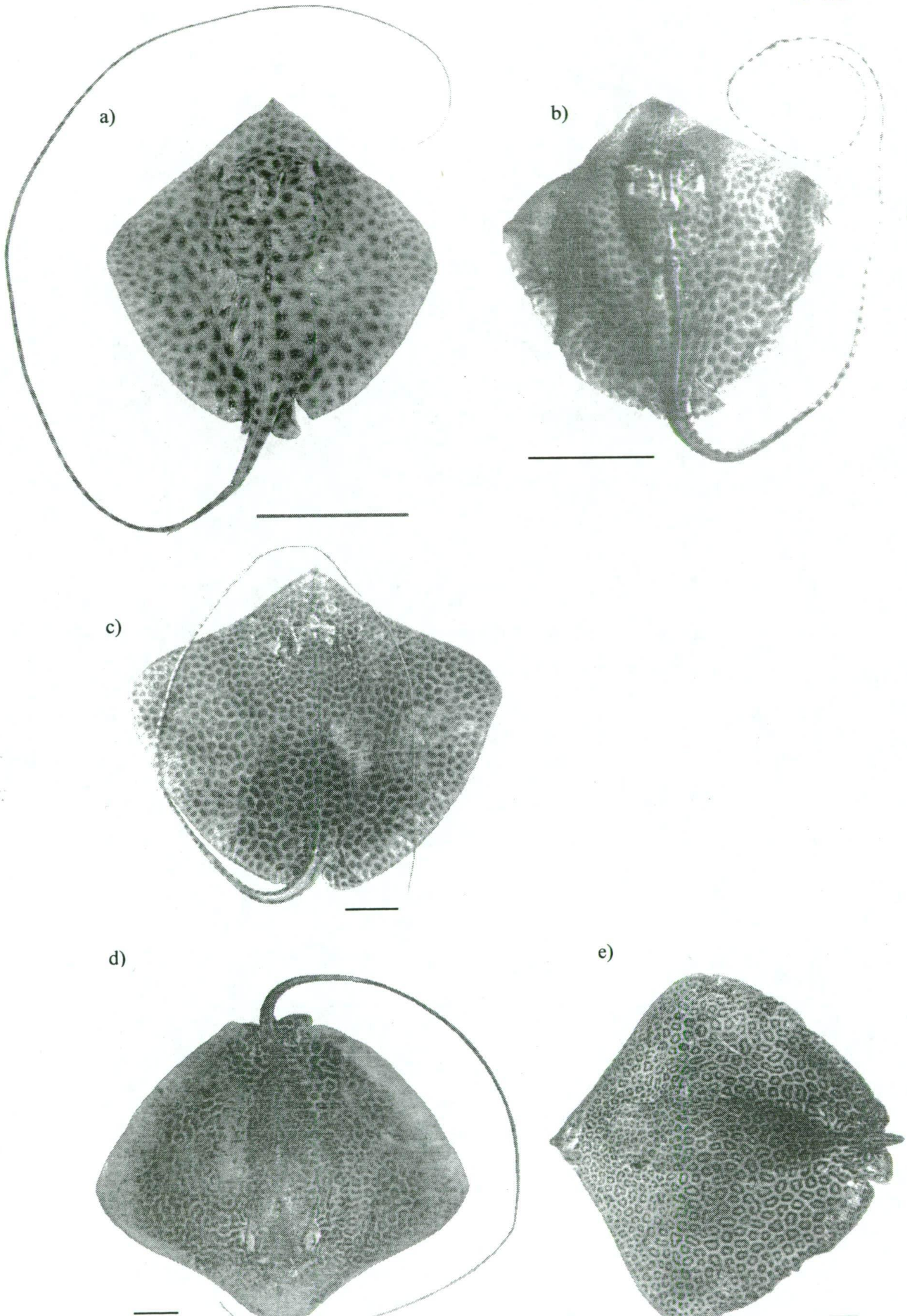

a)
b)
c)
d)
e)

Figure 5.2.24. Representative specimens of *Himantura* sp. A var. 'South Africa' indicating transitional colour pattern with size. a, 340 mm DW (immature male; reproduced from Whitfield 1998: 55); b, 460 mm DW (uncatalogued specimen in the Natal Sharks Board collection; female); c, 704 mm DW (female; reproduced from Wallace 1967: 45, fig. 55); d-e, ~1000 mm DW (mature male and female; live aquarium specimens in Seaworld, Durban). b, d-e: photos and measurements by P. Last).

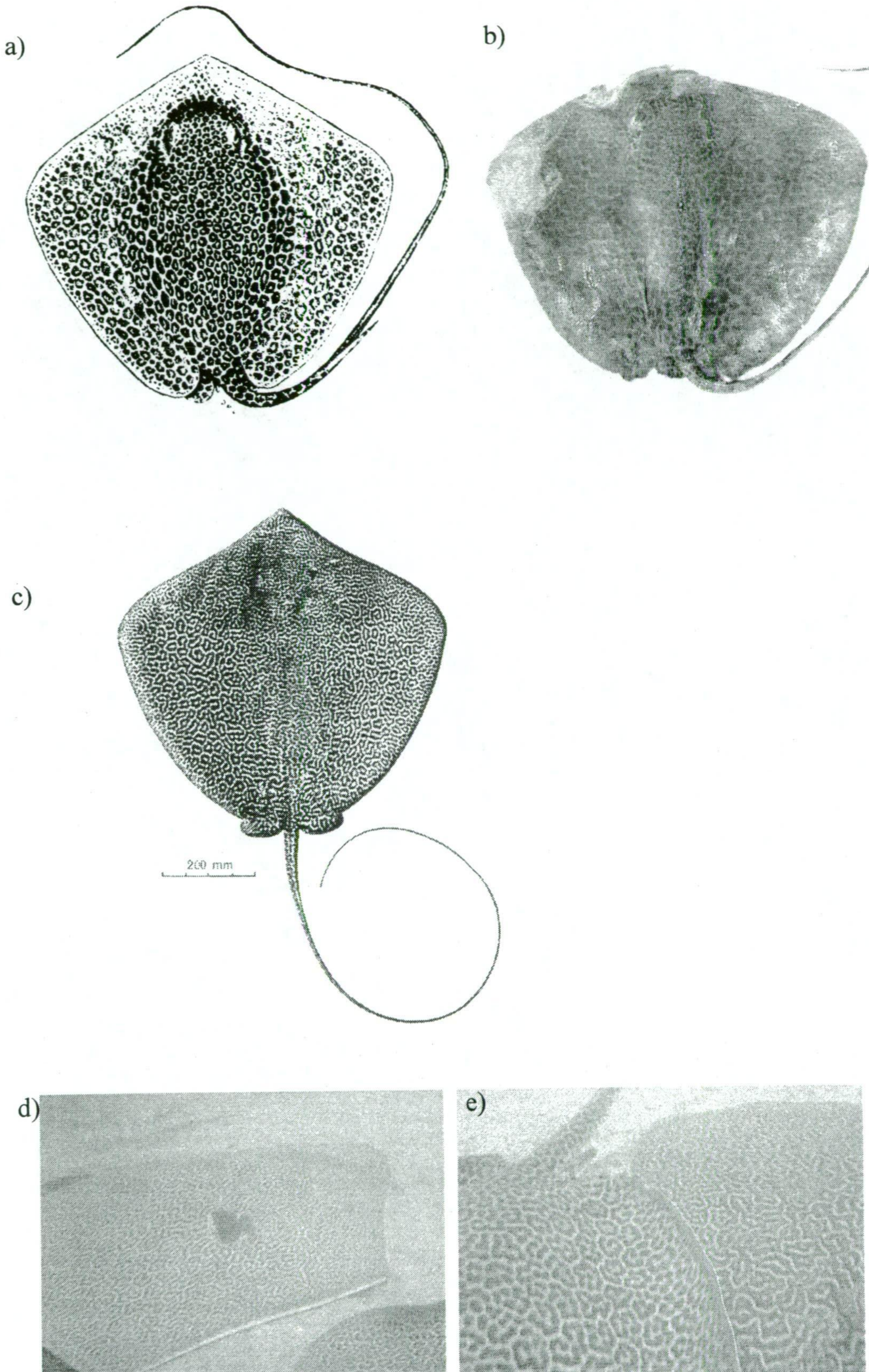
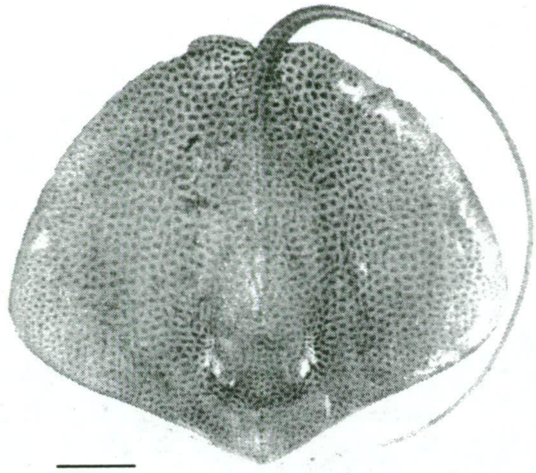
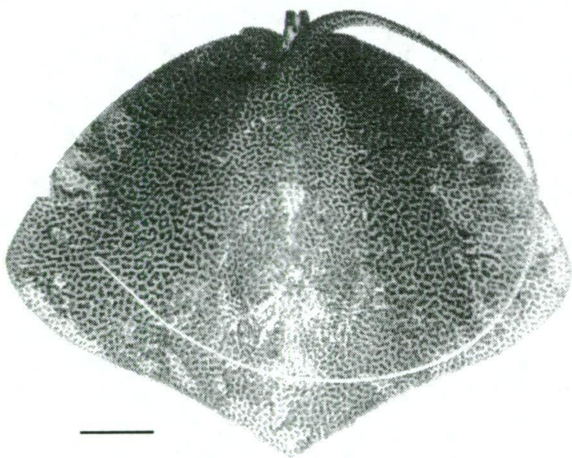

a)
b)
c)
200 mm
d)
e)

Figure 5.2.25. Representative specimens of atypical *Himantura* sp. A indicating intraspecific colour variation of adults in dorsal view. a, 680 mm DW (female; Sandakan, Sabah, Malaysia); b, 864 mm DW (mature male; Tawau, Sabah, Malaysia); c, 1064 mm DW (mature male; Sandakan, Sabah, Malaysia). Bars 10 cm.

a)



b)



c)

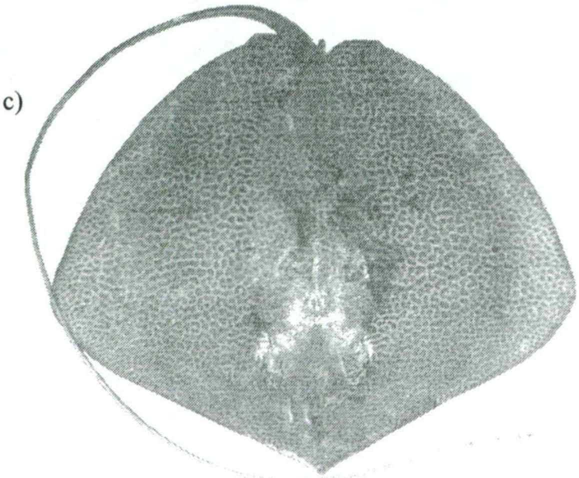
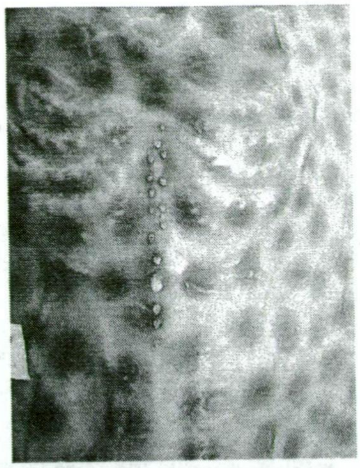


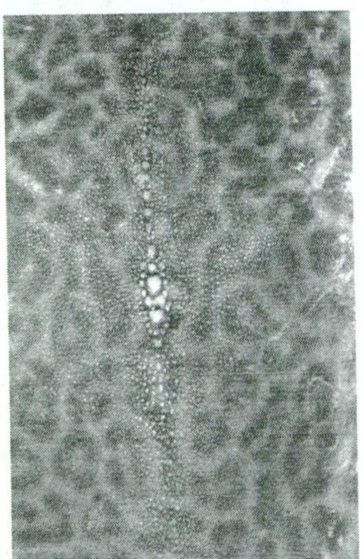
Figure 5.2.26. Representative specimens of *Himantura* sp. A indicating development in squamation. a, 200 mm DW (CSIRO H635.02; female; Northern Territory, Australia); b, 455 mm DW (CSIRO H5478.01; female; Kota Kinabalu, Sabah, Malaysia); c, 805 mm DW (CSIRO H5284.05, parts only; female; Kota Kinabalu, Sabah, Malaysia).

a)



b)

c)



Colour. — In fresh, entire disc diffuse with moderately large dark brown polygonal spots in young; large (>550 mm DW) specimens with thick dark brown irregular rings (rings often incomplete, with open ends), each ring yellowish inside - resembling markings on leopards. Ventral disc surface uniformly pale. Tails of young with spots on each dorsolateral surfaces from its base to sting base, entirely banded behind the sting, with alternating dark and pale (white) rings; ventral surface from tail base to sting base uniform pale. Dark and pale rings almost equal in width nearer sting base, dark rings becoming wider (almost 2 times) than pale ring nearer tail tip. Larger specimens and adults, tail with fine dark brown reticulations on a pale (whitish) background.

Spots becoming 'hollowed' with size (Fig. 5.2.23), even those on the tail base. Spots and rings largest along trunk, gradually decreasing towards disc edge.

Skeletal morphology. — Neurocrania of 447 mm DW female (Figs. 3.2.7v, 3.2.8u), and 870 mm DW mature male (Figs. 3.2.7w, 3.2.8v) with moderately elongate nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval, internasal broad; fontanelle triangular-shaped, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen anterior optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate and robust, basally triangular and posteriorly bluntly pointed; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commisure relatively narrow.

Scapulocoracoid (Fig. 3.2.10s) relatively broad, moderately high, posterior part weakly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to narrow articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle moderately high, 2-2.5 times as high as long;

mesocondyle long and narrow, separated from metacondyle by weak notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11r-s) narrowly arched, relatively thick, median prepelvic process present, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium of mature male (Fig. 3.2.12c; disc width not available) relatively simple; 3 basal segments; beta cartilage present as a separate element, merging posteriorly with axial cartilage; dorsal marginal cartilage broad, paddle-shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, suboval rectangular, and scoop-shaped; terminal tip of axial cartilage short, spatula-like; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of mixopterygial tip, and narrowly extending to lateral surfaces.

Size. — Birth size around 200 mm DW; length at first maturity (males) between 700 and 800 mm DW. A 338 mm DW male specimen (CSIRO H3863.02) was determined as being an immature (maturity stage 2), while a male specimen (specimen not saved; Fig. 5.2.25b) 864 mm DW, as mature (maturity stage 4). Females reaching to 1105 mm DW, as based on a specimen (CSIRO H2903.01) caught from the Gulf of Carpentaria in Northern Territory, Australia.

Etymology. — Nil.

Common name. — Leopard whipray (Last & Stevens 1994), after the leopard like markings on the dorsal surface of large (>550 mm DW) specimens.

Distribution. — India (Lower Bengal), Africa (Natal coast), Australia (inner continental shelf off northern Australia; Torres Strait), New Guinea, Indonesia, Malaysia (e.g. Blyth 1860; Wallace 1967; Gloerfelt-Tarp & Kailola 1984; Compagno 1986).

Comparisons. — *Himantura* sp. A is closest to *H. uarnak* Forsskål, and *H. undulata* (Bleeker), all three with dorsal disc colour patterning (spots or reticulations), similar in overall disc shape. This species is particularly unique in its squamation (arrangement of the midscapular denticles), and in the presence of leopard-like markings on the dorsal surface of large specimens and adults. The birth size is also smallest among the three.

The rate of squamation in this species is rather slow compared to the other two closely related species. Newborns are either totally smooth on the back, or with only a few denticles on the nape (most still embedded in skin), and specimens with size about 500 mm DW are still sparsely covered with denticles.

The midscapular denticles of this species consist of two broad heart-shaped denticles, and are anteriorly preceded by a row of enlarged widely spaced narrow heart-shaped denticles in the primary denticle band, followed by a row of smaller denticles posteriorly.

Remarks. — This new species has been described previously, although erroneously misidentified, either in part or entirely, as one of the following similarly patterned (spotted and/or reticulated) species, i.e. *Himantura fava* (Annandale) (synonymized with *H. undulata*, this study; see also remarks under heading of *H. undalata*), *H. uarnak* (Forsskål), or *H. undulata* (Bleeker), and hence, demonstrating the confusion regarding the taxonomy of patterned stingrays in particular.

The species, described and illustrated in considerable detail as *H. undulata* by Last and Stevens (1994), and later by Last and Compagno (1999), is non Bleeker. Instead the name *undulata* have been wrongly applied to denote the previously undescribed species (see also remarks under heading of *H. undulata* species description). It is noted that since the publication of these two major references (P. Last pers. comm.), more specimens representing the different life stages of the species as described by Last and Stevens, and Last and Compagno, have been obtained. The collection of additional materials has made it possible to understand better the ontogenetic character changes, particularly regarding gradients in squamation and dorsal disc colour patternings (as given earlier in the species description), as well as distinguishing it from the other similarly patterned species.

Hence, this species is recognized as different from *H. undulata* (Bleeker), and is a separate valid species. However, the common name 'leopard whipray' proposed by Last and Stevens, is retained, as it reflects the unique dorsal disc colour pattern of adults of this species.

Apart from the typical 'leopard' form, two other atypical forms are herein recognized, and are tentatively named the 'fine leopard' form (Fig. 5.2.25), and the 'South African' variety (Fig. 5.2.24). Representatives of former have been recorded from the same areas as the typical form, whereas the latter, as the name suggests, have only been recorded from South Africa.

The placement of these forms within this species is primarily based on results obtained from molecular data of the fine leopard form, i.e. DNA analysis of the 16S and cytochrome *b* genes resulted in representatives of the form clustering among *H.* sp. A (this study; Chapter 4). The fine leopard, and the South African forms each have similar colour patterns and arrangement of midscapular denticles as that seen in the typical form. However, apart from the molecular data of the fine leopard, this and the other form are presently only known from colour photographs of large specimens.

A possible name for this species is *Himantura russellii* (Gray 1834). The names *Trigon russellii* Gray 1834 and *Trygon russelli* Gray 1834, listed in the synonymy, are both preceded with a question mark, to indicate that the paper was not seen, where, unfortunately, attempts to obtain the paper were unsuccessful. Both names (note differences in the spelling of the genus and species) were first listed by Gray

(1851) under the synonymy list of *T. uarnak*, with 'Gray and Hardwicke' given as the authors, but with only anecdotal information regarding those publications, and without any dates. Gray also did not provide any description (of the *T. uarnak*) whatsoever, thus it remains unclear how he originally described *T. russellii*. The proper publication citation including the dates for these papers were obtained through the 'search reference' feature in the on-line Catalog of Fishes (Eschmeyer On-Line ver. February 15, 2002).

Hence, the reason the name *Himantura russellii* (Gray) is mentioned as a possible name for this species is mainly based on the description of the species by Blyth (1860). Blyth's species description of *T. russellii* under the same heading appear to be partly a misidentification of *H. undulata* (see also remarks under that species heading, this study).

In particular are his references to the colour patterns, '... covered above with large round dark spots, a few which are generally confluent: tail banded throughout ... in large specimens (3 ft. across) (~90 cm DW) the spots continue as strongly marked as in the young, and are then more or less pale-centred, forming, distinct rings more or less perfect in some specimens...'

Blyth again described the species under the heading of *T. uarnak*. Under this species heading, the squamation pattern was indicated, '... of a size at which *T. russellii* has few and sparse tubercles on the back .... *T. uarnak* has the dorsal tubercles fully developed, and a broader band of them at base of tail than is seen in *T. russellii* of more than double the size ...'.

Another example of misidentification of the species is by Wallace 1967. Apparently, the species identified as *H. uarnak* is the 'South African' variety. In particular is his mention of the presence of 'a median row of small tubercles... more obvious in small specimens, occurs above the branchial region and terminates in two enlarged tubercles above the shoulder. Smaller widely spaced denticles occur on the interorbital and along the midline of the back, terminating on or before the base of the tail. The rest of the disc and pelvic fin are naked.' The row of small tubercles however, was not evident from the illustration of a 704 mm DW female specimen (Fig. 5.2.24c).

There exists many other works with possible misidentifications, or misidentification in part, of this species. Based solely on the given distribution list, and compared against the known and/or perceived distribution of this species, some of these are listed in the following: Richardson 1846 (listed *T. uarnack* from Sea of China, Indian Ocean, Red Sea, Cape of Good Hope; misspelling of species name), Sauvage 1891 (listed *H. uarnak* from Madagascar), Regan 1908 (listed *Dasybatis uarnak* from Natal), Garman 1913 (listed *Dasybatus Himanturus uarnak* from Indian Ocean, Red Sea and East Indies), Fowler 1928 (listed *Dasyatis uaranak* from Bombay, Philippines and Sumatra), and McCulloch 1929 (listed *Himantura arnak* from north Australia).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

a. H. sp. A: Leopard whipray (typical 'leopard' form)—
CAS 213280 (Thailand); CSIRO H635.02, CSIRO H3863.01, CSIRO H3863.02, NTM S.10765.002 (Arafura Sea, NT, Australia); CSIRO H2903.01, CSIRO H3903.02[b] (G of Carpentaria, QLD, Australia); CSIRO H4131.01 (Manila, Philippines); CSIRO H5284.05[e], CSIRO H5478.01[e], UMS MMKK136[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H5585.02 (off Beruwala, Sri Lanka); RMNH 2473[c] (unspecified locality); SUML BRU084[c] (Philippines); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

b. H. sp. A: Leopard whipray (atypical 'fine leopard' form)—
CSIRO H5479.08[b,c], UMS MMSK(c4)[e] (Sandakan, Sabah, Malaysia); field photographs of adult specimens[c] (Sabah and Sarawak, Malaysia); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

c. H. sp. A: Leopard whipray (var. 'South Africa')—
Sharks Board collection[c] (Natal, South Africa); live Sea World aquarium specimens[c] (Durban, South Africa).

Himantura sp. B

Arabian banded tail

Figure 5.2.27; Tables 5.2.15–5.2.16

Synonymy. —

Dasyatis jenkinsii (not Annandale): Wallace 1967, 47, fig. 23 (description, illustration of a 437 mm disc width immature male, misidentification). Localities: off Natal beach, Durban Bay, and in 23 fathoms off Amatikulu Bluff, South Africa.

Himantura gerrardi (not Gray): Compagno 1986, 139, fig. 30.9 (brief description, illustration of a 190 mm disc width female, misidentification in part). Localities: Eastern Cape to Natal and Mozambique.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, robust, preorbital snout moderately long, with a small apical lobe, anterior disc margin almost straight, lateral apices moderately angular. Dorsal surface of disc uniform grey to light brown, with prominent white edges; ventral surface of disc pale whitish with light brown patches present throughout, specimens less than 400 mm disc width sometimes with narrow yellowish-brown margins of the ventral surface, beginning apex of pectorals, continuing to posterior tip of pectorals; tail conspicuously banded in neonates and juveniles, bands becoming obscured with age (>250 mm disc width), tail blackish in adults. Denticle band along mid-trunk well-developed, and tail rugose even in young (ca. 400 mm disc width), broad heart-shape suprascapular denticle conspicuous, thorns absent.

Description. — Disc rhomboidal, width 1.02-1.05 times length; robust, center raised at midscapular, maximum disc thickness 0.12-0.17 in disc width (DW); preorbital snout moderately long, with a small apical lobe, angle 114-120.5°; anterior margins of disc almost straight, lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.2.27). Pelvic fins moderately long, 18.6-21.3% DW; width across base 14.0-15.6% DW. Claspers of adult male (CSIRO H5700.01; figure not shown) long and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle short, about 1/3rd of clasper length on its outer margin, weak notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.24-2.58 times disc width; base narrow, subcircular in cross-section, width 1.07-1.58 times height at base.

Snout moderately long, depressed; preoral snout length 2.98-3.44 times mouth width, 2.59-2.69 times internarial distance, 21.9-22.7% DW; direct preorbital snout length 1.51-1.57 times interorbital length, horizontal length 1.41-1.53 times interorbital length; snout to maximum disc width 39.2-42.6% DW; interorbital space slightly convex; eye moderately large, diameter 38-62% spiracle length; orbits slightly protruded, diameter 0.68-0.98 in spiracle length, interorbital distance 2.07-3.22 times orbit. Spiracles rectangular-shaped, size almost equal to orbits, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak double concavity, length 0.41-0.53 in internasal distance; internasal distance 0.49-0.51 of prenasal length, 1.87-2.42 times nostril length. Nasal curtain skirt-shaped, relatively narrow, width 1.66-1.78 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

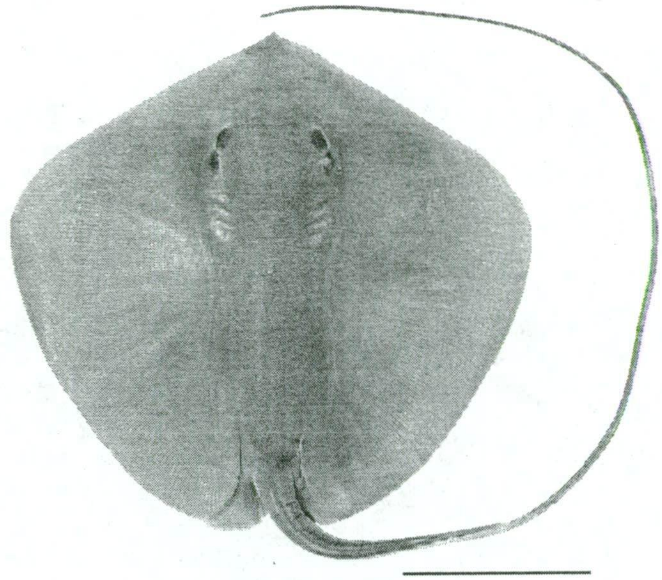
Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2 short, well-developed papillae, rounded distally, longitudinally flattened, subequal in size.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth row counts not available.

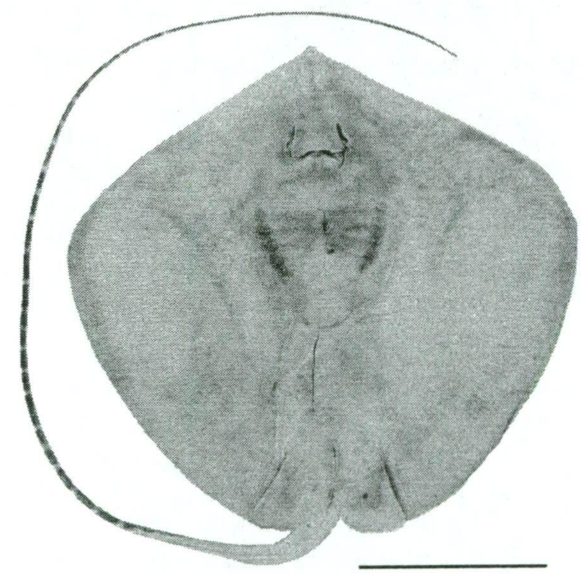
Gill opening margins smooth, straight; length of first gill slit 1.13-1.56 times length of fifth, 0.38-0.47 of mouth width; distance between first gill slits 2.47-2.62 times internasal distance, 0.45-0.47 of ventral head length; distance between fifth gill slits 1.57-1.64 times internasal distance, 0.28-0.30 in ventral head length.

Figure 5.2.27. Representative specimen of *Himantura* sp. B in dorsal and ventral views (a-b), and close-up of scapular denticles (c). BPBM 33201(2of2) (246 mm DW; female; Persian Gulf, Kuwait). a–b: photos by T. Carter. Bars 10 cm.

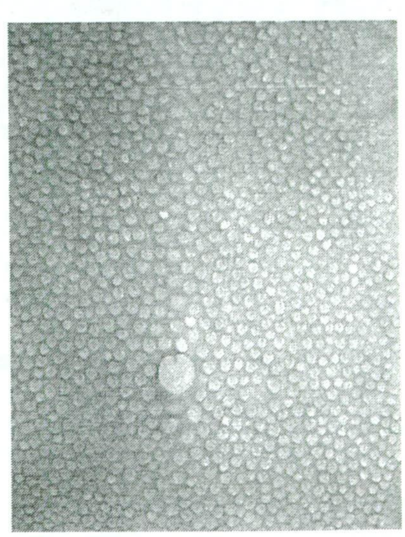
a)



b)



c)



Squamation. — Stages of squamation with narrow size ranges; secondary denticle band well-developed, and tail rugose even in young (ca. 400 mm DW); posterolateral series of denticles present. Development of secondary denticle band simultaneous with centre of disc appearing raised.

Stages 0-1: from birth (ca. 150-170 mm DW) — Disc entirely smooth, or with 1-2 small, broad heart-shape suprascapular denticles (3 mm long). Primary median denticle band present as a row of denticles anterior of suprascapular denticle; size smaller than suprascapular denticles.

Stage 2: (ca. ?200 mm DW) — The question mark denotes the likely size for this stage, as there is no representative specimen available for study; the smallest specimen with a well-developed denticle band (squamation Stage 4) is 246 mm DW (BPBM 33201 [1 of 2]; female).

Stage 4: (>240 mm DW) (Fig. 5.2.27) — Secondary denticle band well-developed, with well-defined margin, extending as a continuous, longitudinal band along trunk, terminating at tail base.

Primary denticle band becomes obsolete at this stage.

In two larger specimens (BPBM 29480 and MTUF 20642) 325 mm DW and 414 mm DW, respectively, secondary denticle bands continuous to tail, tail naked below from tail base to sting base. Band extended to just anterior of orbits, naked snout ratio 70.7-73.3% in direct preorbital snout length; margin convex anteriorly; width confined to within interspiracular distance; narrowing very gradually posteriorly from mid-disc, before continuing to tail. Second half of tail along mid-dorsal beginning base of sting tip, denticles cone-shaped; laterally (both sides) heart-shaped, pointed tip elevated; denticle uniform size on margin, the large denticles elevated.

Denticles in band compact, closely-set, size uniform in young; small- and large-size denticles interspersed (not imbricated) with age; the largest size along mid-trunk and around tail base, decreasing towards tail tip; denticles minute along tail. Outside of denticle band, skin smooth, without denticles, except on narrow margin of pectorals, fine spiny denticles comprising the posterolateral series (see Chapter 2) present, appearing as a narrow (2 mm wide) dark margin in all three specimens with developed secondary denticle band.

Stages 3, 5 and 6 not applicable for this species.

Three specimens (including neonates) with one elongate stinging spine, another two with two stings; missing (removed) in others. Sting of neonates with blunt tip, enveloped by skin.

Meristics. — Total pectoral-fin radials 125-129 (n=4); propterygium 48-52, mesopterygium 17-20, metapterygium 58-60; pelvic-fin radials 25-29; vertebral segments 108-112, monospondylous 43-45, prespine diplospondylous 63-68 and postspine diplospondylous 0.

Colour. — In fresh (live aquarium specimen in Durban, South Africa; photo by P. Last), dorsal surface of disc uniform grey to light brown, with prominent white edges; ventral surface of disc, including pelvic fins and tail base, pale with light brown patches present throughout; smaller specimens (<500 mm DW) with narrow yellowish-brown margins of the ventral surface, beginning apex of pectorals, continuing to posterior tip of pectorals, apparently absent in larger specimens (>500 mm DW). Tail conspicuously banded in neonates and juveniles (of up to 170 mm DW), with more or less equally wide white and blackish bands alternating from beyond sting base; band disappearing, especially on dorsal half of tail, although still evident in larger juveniles (246 mm DW) (Fig. 5.2.27); becoming uniform dark brown to blackish on dorsal half, and pale (whitish) ventrally. Orbits whitish below, as well as the dorsal margins of the spiracles; evident also in preserved specimens.

Colour of dorsal disc surface of four preserved specimens are all yellowish brown dorsally, whitish ventrally; two specimens (BPBM 33201[1of2] and BPBM 33201

[2of2]) evidently with faded brown specks over entire dorsal disc surface, more so along the trunk and adjacent areas, but not on disc margins.

Skeletal morphology. — No dissections were carried out. However, based on x-ray plates, the shape of the neurocranium is of a 'typical' *Himantura*.

Size. — Birth size around 150-170 mm DW; length at first maturity (males) between 500 and 600 mm DW. A 325 mm DW male specimen (BPBM 29480) was determined as being an adolescent (early maturity stage 3), while a male specimen (in the Natal Sharks Board; temporary registration number 'DUR 16'; right clasper donated to CSIRO by G. Cliff, CSIRO H5700.01) 620 mm DW, as mature (maturity stage 4). Females probably mature around 600 mm DW (A. Moore, pers. comm.), reaching to 700 mm DW, as observed in an uncatalogued female specimen in the South African Museum collection (digital colour photo courtesy of P. Last).

Etymology. — Nil.

Common name. — Arabian banded tail.

Distribution. — Recorded from Kuwait Bay, Bahrain fish market (Persian Gulf) in Kuwait; Oman (e.g. Randall 1995), and southeastern South Africa, in shallow bay and estuaries, and offshore down to 50 m (e.g. Wallace 1967; Van der Elst 1981; Compagno 1986; Compagno *et al.* 1989; Stehmann 1995; J. Randall, pers. comm. 2001).

Comparisons. — This species is very similar to *Himantura gerrardi* Gray, and to two other unidentified species tentatively named as *H.* sp. C (Pakistan whipray) and *H.* sp. D (short-tail whipray). *Himantura* sp. B is distinguished from these species by a combination of characters, i.e. disc about as wide as long, squamation (including shape of suprascapular denticles, i.e. broad heart-shape; denticles in band largish, with small- and large- size denticle interspersed; fastest squamation rate, i.e. secondary denticle band well-developed in relatively small specimens), and colouration of dorsal disc, including pattern of tail banding, i.e. disc uniform plain, tail banded in neonatal and juveniles, band disappearing with age; fine spiny denticles comprising the posterolateral series (see Chapter 2) present in this species, absent in others.

Remarks. — The existence of this species was first known to P. Last (pers. comm.) from Kuwaiti specimens sent in by J. Randall. Apparently, it is frequently misidentified as *H. gerrardi* and/or *H. bleekeri*. It is noted herein that *H. bleekeri* is considered as a senior synonym of *H. uarnacoides* (this study).

The distribution of this new species in southeastern South Africa is also primarily attributed to observations by P. Last and J. Randall (pers. comm.), both of whom have seen live aquarium specimens in Durban. Hence, based on literature review (e.g. Wallace 1967; Van der Elst 1981; Compagno 1986; see also e.g. Nishida 1990 on specimens identified as *H. bleekeri*) to obtain an insight into the South African elasmobranch fisheries components, it appears the species as widely misidentified in this subregion. For example, the illustration of a 437 mm DW *Dasyatis jenkinsii* (=*H. jenkinsii*) in Wallace (1967), indicate a banded-tail stingray, with well-developed secondary denticle band and presence of a large suprascapular denticle, and the disc shape similar to this new species; as noted by Wallace, 'tail in embryos and juveniles with alternating light and dark bands'.

Moreover, according to Wallace (1967) (of the specimens he identified as *Dasyatis jenkinsii*), a gravid female 800 mm DW containing two embryos was netted in Durban Bay in February 1964; and two males 710 and 735 mm DW were already sexually mature.

A 325 mm DW male specimen (BPBM 29480) examined in this study, was determined as being an adolescent (maturity stage 3), based on its clasper development. Additional specimens are required to address other life history parameters, and characters such as squamation, ventral lateral line canal patterns, and skeletal structures (i.e. neurocranium, scapulocoracoid, mixopterygium).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CSIRO H5700.01[b,c] (South Africa); BPBM 21367[b] (Gulf of Oman, Oman); BPBM 33201(1of2), BPBM 33201(2of2) (Persian Gulf, Kuwait); BPBM 29480 (Persian Gulf, Bahrain); MTUF 20642 (Arabian Sea).

Himantura sp. C

Pakistan whipray

Figure 5.2.28; Tables 5.2.17-5.2.18

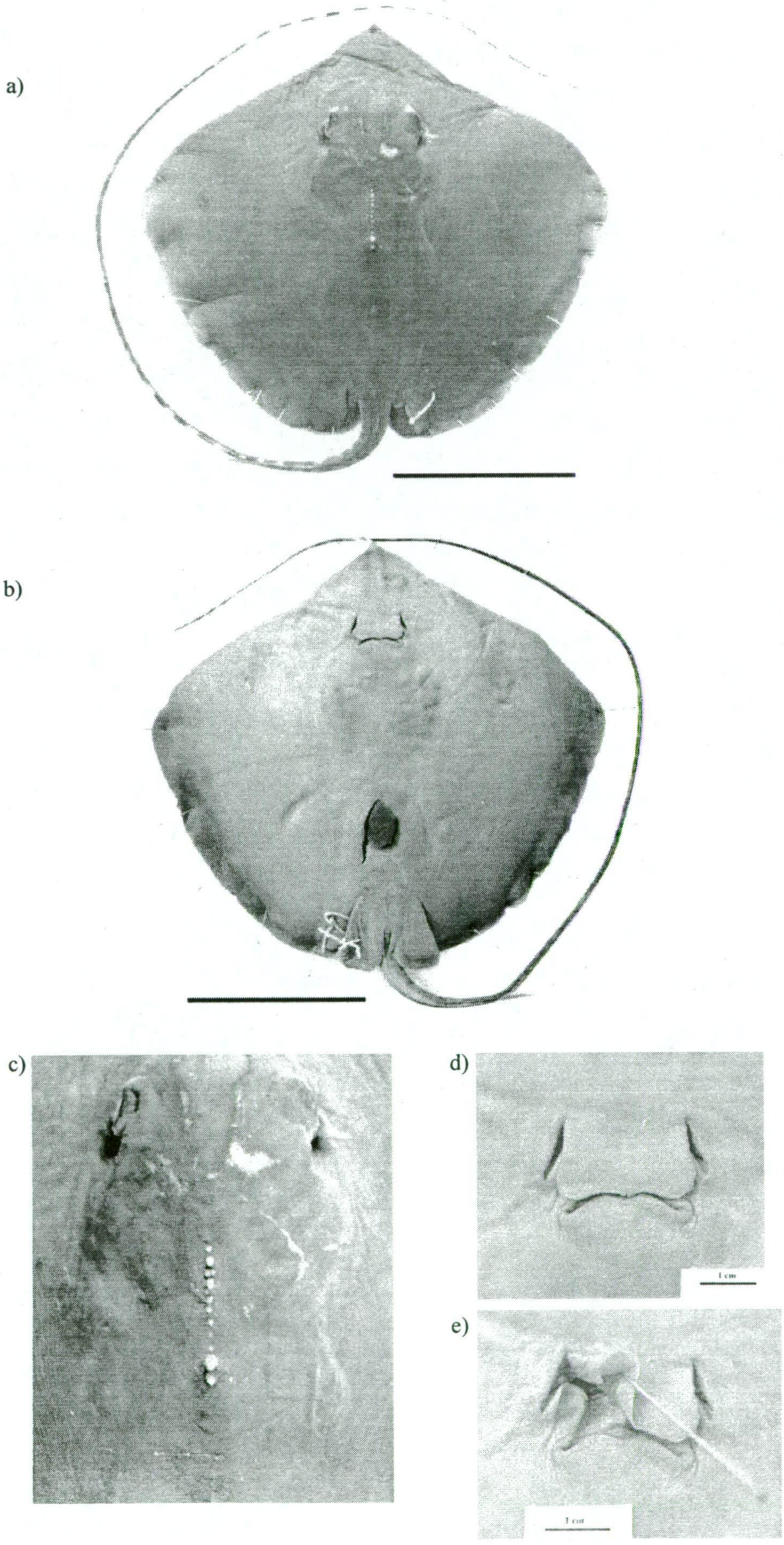
Synonymy. —

Nil.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, moderately raised at center, preorbital snout moderately long, with relatively narrow and distinct apical lobe, anterior disc margin concave, lateral apices moderately angular. Dorsal surface of disc uniform light brown; ventral surface uniform pale (whitish), with weakly-defined, moderately broad yellowish-brown margins beginning apex of pectorals, continuing to posterior tip of pectorals; tail uniform light-brown on dorsal surface between tail base and sting base, banded beyond sting base; bands obscured with age, becoming blackish with very faint pale rings on dorsal surface. Denticle band along trunk and tail sparse even at 325 mm disc width, small seed-shape suprascapular denticles, thorns absent.

Description. — Disc rhomboidal, width 1.05-1.13 times length; mid-scapular moderately raised, maximum disc thickness 0.09-0.14 in disc width (DW); preorbital snout moderately long, pointed apical lobe relatively narrow and distinct, angle 113-123^{o}; anterior margins of disc concave, lateral apices moderately angular; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.2.28). Pelvic fins moderately long, 16.6-20.5% DW; width across base 11.7-14.7% DW. Mature male specimen not available for examination of clasper structure. Tail slender and whiplike, tapering gently towards sting and tail tip, becoming flattened towards tip, length 2.22-2.62 times disc width; base slightly depressed in cross-section, width 1.26-1.70 times height at base.

Figure 5.2.28. Representative specimen of *Himantura* sp. C in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of primary denticle band; d, close-up of oronasal; e, oronasal (nasal curtain folded back). LACM 38312.027(1of2) (251 mm DW; immature male; Baluchistan, Pakistan). Bars 10 cm.


a)
b)
c)
d)
e)
1 cm
1 cm

Snout moderately long, depressed; preoral snout length 3.06-3.84 times mouth width, 2.29-2.60 times internarial distance, 20.5-23.6% DW; direct preorbital snout length 1.70-1.92 times interorbital length, horizontal length 1.56-1.80 times interorbital length; snout to maximum disc width 39.2-44.0% DW; interorbital space flat; eye moderately large, diameter 41-65% spiracle length; orbits slightly protruded, diameter 0.73-1.11 in spiracle length, interorbital distance 1.66-2.23 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, slit-like, laterally expanded, outer margin with a weak double concavity, length 0.47-0.55 in internasal distance; internasal distance 0.52-0.57 of prenasal length, 1.82-2.14 times nostril length. Nasal curtain skirt-shaped, relatively narrow, width 1.54-1.79 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly double concave.

Mouth arched; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2-4 papillae; medial pair simple, rounded distally, subequal in size and almost three times larger than outer pair, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth row count not available.

Gill opening margins smooth, straight; length of first gill slit 1.41-1.90 times length of fifth, 0.39-0.55 of mouth width; distance between first gill slits 2.12-2.34 times internasal distance, 0.43-0.46 of ventral head length; distance between fifth gill slits 1.34-1.48 times internasal distance, 0.27-0.30 in ventral head length.

Squamation. — Stages of squamation with broad, overlapping size ranges; secondary denticle band on dorsal surface of disc slowly developing; rate of denticle band development appear faster in females.

Stage 0: from birth (ca. 170-200 mm DW) — Disc entirely smooth, or with 1-2 small, seed-shaped suprascapular denticles.

Stage 1: (ca. 230-270 mm DW) (Fig. 5.2.28) — Development of primary denticle consisting of small (smaller than suprascapular denticles) seed- and narrow heart-shaped denticles; arranged in a narrow series (1-2 rows) in the area around the nuchal region. Band becoming obscure with age.

Stage 2: (ca. 250-325 mm DW) — Initial stage for development of secondary denticle band; onset around primary band, forming scapular patch, followed by development of cranial patch; margins of band weakly-defined, denticles embedded under skin. During mid- stage, a few spinulose (minute cone-shaped) denticles developing along dorsal surface of tail on its posterior half. Denticles in band compact, closely set, small- and large- size denticles interspersed (length of larger denticles 1.3-1.5 mm); uniform size along margins.

Stage 4: (?>500 mm DW) — The question mark denotes the likely size for this stage, as there was no representative specimen available for study; the denticle band as seen in the largest specimen (squamation Stage 2), is likely to develop into a continuous, longitudinal denticle band with weakly-defined margins.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine present.

Meristics. — Total pectoral-fin radials 127-135 (n=6); propterygium 51-54, mesopterygium 15-21, metapterygium 58-62; pelvic-fin radials 24-30; vertebral segments 102-111, monospondylous 41-47, prespine diplospondylous 55-68 and postspine diplospondylous 0.

Colour. — Disc uniform light brown, plain without spotting; ventral surface uniform pale (whitish), with weakly-defined, moderately broad yellowish-brown margins beginning apex of pectorals, continuing to posterior tip of pectorals, including free rear tip of pelvic-fins. Tail uniform light brown on dorsal surface between tail base and sting base, banded beyond sting base; ventrally plain between tail base and sting base, weakly banded beyond sting base. White spots present along dorsolateral surface between tail base and sting base, spots evenly spaced between each other, until at distance about 1/3rd to middle between sting tip and tail tip, 'twin-spots' (two spots joined together) present; 3 or more pairs of twin-spots frequently present. Tail becoming blackish, with very faint pale rings on dorsal surface with age (from about 325 mm DW).

Skeletal morphology. — No dissections were carried out. However, based on x-ray plates, the shape of the neurocranium is of a 'typical' *Himantura.*

Size. — Birth size around 170 mm DW; length at first maturity unknown. Male specimens between 250 and 268 mm DW, are immature (maturity stage 2). A larger female, 325 mm DW (LACM 38133-48[3of4]) is probably not mature.

Etymology. — Nil.

Common name. — Pakistan whipray.

Distribution. — Recorded from Pakistan (Sind, 3 to 4 km west of mouth of Turshian Creek; and Baluchistan, Sonmiani Bay).

Comparisons. — This species is very similar to *H. gerrardi* Gray, and to two other unidentified species, tentatively named as *H.* sp. B (Arabian banded tail) and *H.* sp. D (short-tail whipray). *Himantura* sp. C is distinguished from these species by a combination of characters, i.e. disc slightly wider than long, mid-scapular denticles small, seed-shaped; denticles in band moderately sized; squamation rate relatively slow (similar to rate of *H. gerrardi*), disc uniform plain, and tail prominently banded in neonatals, disappearing with age. Morever, the tail appears thicker, not as filamentous as in the other three species.

Remarks. — The existence of this species is known from a few specimens from two localities in Pakistan. The specimens, on loan from The Natural History Museum of Los Angeles County, were previously identified as *H. gerrardi*. Records from elsewhere in the subregion, may be a misidentification in part (e.g. Anon. 1955, on *H. uarnak*), or not recorded at all (e.g. Bianchi 1985). Additional specimens are required to address the information not available based on existing specimens alone.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CAS 29630, CAS 29646 (off Karachi, Pakistan); LACM 38133.048(3of4), LACM 38133.048(4of4) (Sind, Pakistan); LACM 38311.034(2of2), LACM 38312.027(1o2), LACM 38318.011(3of4), LACM 38318.011(4of4) (Baluchistan, Pakistan).

Himantura sp. D

Short-tail whipray

Figure 5.2.29; Tables 5.2.19-5.2.20

Synonymy. —

Dasyatis uarnak (not Forsskål): Jones & Kumaran 1970, fig. 16 (described 2 specimens 425 and 480 mm disc width, compiled distribution partly in error).

Himantura gerrardi (not Gray): Ishihara *et al.* 1998, 44, pl. 3 (brief description of two specimens, one figured MTUF 30005, misidentification in part). Localities: Diamond Harbour, and Farakka, India; caught August 1997 and December 1996, respectively).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape rhomboidal, center raised at midscapular, preorbital snout moderately long, slightly convex, with a distinct apical lobe, anterior disc margin almost straight, lateral apices narrowly rounded. Dorsal surface of disc uniform light brown, without any spotting; ventral surface of disc uniform pale (whitish), with broad yellowish brown margins beginning at lateral apices of pectorals, continuing to posterior tip of pectorals, including free rear tip of pelvic fins. Tail dark brownish to blackish, with evidence of weak dorsal banding behind sting, ventrally plain. Denticle band along mid-trunk quite well developed by 240 mm disc width.

Description. — Disc rhomboidal, width 1.01-1.08 times length; robust, center raised at mid-scapular, maximum disc thickness 0.11-0.16 in disc width (DW); preorbital snout moderately long, slightly convex, with a distinct apical lobe, angle 117.5-124$^{\mathrm{o}}$; anterior margins of disc almost straight, lateral apices narrowly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.2.29). Pelvic fins moderately long, 18.5-22.3% DW; width across base 14.3-15.6% DW. Mature male specimen not available for examination of clasper structure. Tail slender and whiplike, tapering gently toward sting and tip, length

2.43-3.57 times disc width; base slightly depressed in cross-section, width 1.47-1.87 times height at base.

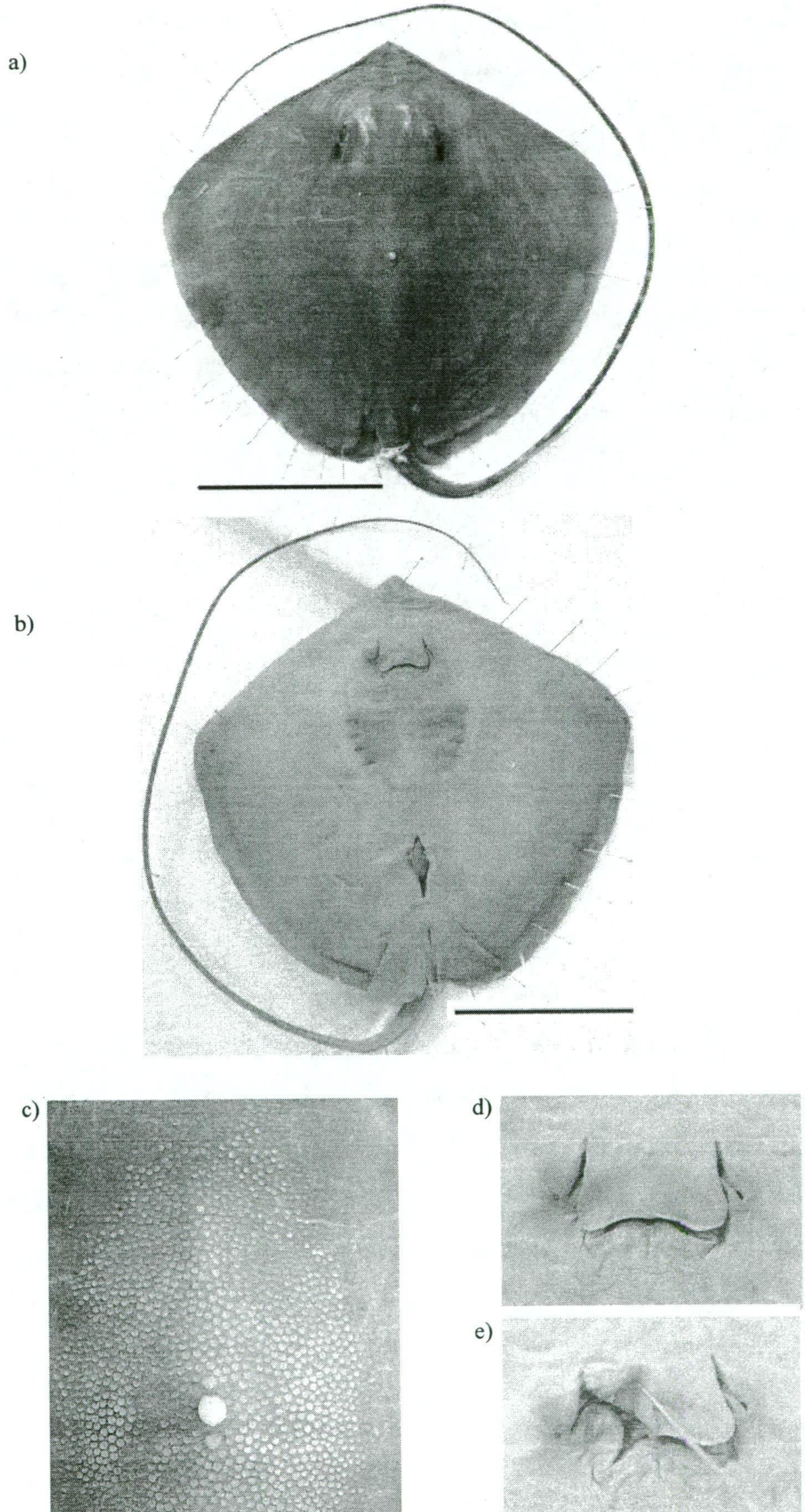
Snout moderately long, depressed; preoral snout length 2.88-3.64 times mouth width, 2.24-3.47 times internarial distance, 20.5-23.6% DW; direct preorbital snout length 1.47-1.88 times interorbital length, horizontal length 1.37-1.79 times interorbital length; snout to maximum disc width 35.9-43.2% DW; interorbital space flat; eye moderately large, diameter 0.54-0.66 in spiracle length; orbits slightly protruded, diameter 0.78-1.17 in spiracle length, interorbital distance 1.72-2.58 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, slit-like, laterally expanded, outer margin weakly concave, length 0.45-0.59 in internasal distance; internasal distance 0.37-0.58 in prenasal length, 1.69-2.21 times nostril length. Nasal curtain skirt-shaped, relatively broad, width 1.60-1.98 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth arched; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 4 well-developed papillae; medial pair simple, rounded distally, longitudinally flattened, sub-equal in size and larger than outer pair, closer to each other than outer two; outer pair located at each corner of mouth, widely separated from inner pair.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth row counts not available.

Gill opening margins smooth, straight; length of first gill slit 1.33-1.53 times length of fifth, 0.39-0.46 of mouth width; distance between first gill slits 2.23-2.69 times internasal distance, 0.41-0.48 of ventral head length; distance between fifth gill slits 1.41-1.68 times internasal distance, 0.25-0.30 in ventral head length.

Figure 5.2.29. Representative specimen of *Himantura* sp. D in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of primary denticle band; d, close-up of oronasal; e, oronasal (nasal curtain folded back). LACM 38131.43 (241 mm DW; immature male; Karachi, Pakistan). Bars 10 cm.


a)
b)
c)
d)
e)

Squamation. — Stages of squamation with broadly overlapping size ranges; rate of squamation relatively fast, secondary denticle band quite well developed by 240 mm DW.

Stages 0-1: from birth (ca. ?150-170 mm DW) — The question mark denotes the likely size for this stage, as there was no representative specimen available for study; newborns are likely to with disc entirely smooth, or with 1-3 suprascapular denticle, along a median primary denticle band which becomes inconspicuous with age. Suprascapular denticle square pearl-shaped (3.6-4.7 mm in length).

Stage 2: (ca. 190-250 mm DW) (Fig. 5.2.29) — The initial stage for development of secondary denticle band; the smallest specimen (LACM 38130-47 [2of3]) 198 mm DW, has a scapular denticle patch with denticles on the margins still embedded under skin; minute spinulose denticles developing on dorsal surface of tail, posterior sting. Primary denticle band inconspicuous.

Stage 4: (>240 mm DW) — Secondary denticle band with sharply-defined margin, band continuous along the trunk from interorbital to pectoral-fin insertion in a specimen 241 mm DW (LACM 38130-47 [1of3]). In a larger specimen 421 mm DW (MTUF 30005), band extended on to tail, across entire dorsal surface; anterior margin well forward of orbits, naked snout ratio around 63%; margin broadly rounded anteriorly, distinctly indented anterolaterally, convex beside eyes, width extended outside interspiracular distance, narrowing gradually posteriorly, diverging laterally for a distance equivalent to a spiracle length at pectoral-fin insertion. Outside of denticle band, skin smooth, and without denticles. Denticles in band, closely set, subequal, becoming only slightly smaller along margins.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine present.

Meristics. — Total pectoral-fin radials 127-132 (n=5); propterygium 50-53, mesopterygium 17-21, metapterygium 57-60; pelvic-fin radials 23-30 (n=5); vertebral segments 111-121 (n=4), monospondylous 44-55 (n=5), prespine diplospondylous 64-69 (n=5), and postspine diplospondylous 0 (n=5).

Colour. — Disc uniform light brown, plain without any spotting; ventral surface uniform pale (whitish), with broad yellowish brown margins beginning at lateral apices of pectorals, continuing to posterior tip of pectorals, including free rear tip of pelvic fins. Tail dark brownish to blackish, with evidence of weak dorsal banding behind sting, ventrally plain. White spots present along dorsolateral surface between tail base and sting base; beyond sting, presence of alternating black and white bands on dorsal surface, width of black bands 2-7 times white (pale) bands.

Skeletal morphology. — No dissections were carried out. However, based on x-ray plates, the shape of the neurocranium is of a 'typical' *Himantura.*

Size. — Birth size around 150-170 mm DW; length at first maturity unknown. A male specimen with disc width 241 mm is immature (maturity stage 2). A larger female, 421 mm DW (MTUF 30005) is probably an adolescent (maturity stage 3)

Etymology. — Nil.

Common name. — Short-tail whipray.

Distribution. — Recorded from Sind, Pakistan (coastal waters from 20 km south of Paitiani Creek, to 15 km north of mouth of Turshian Creek, to approximately 6 km south of Hajambro Creek at an offshore distance of about 5-12 km, and from coastal waters south of Karachi, from 6-8 km south of Hajambro Creek to Turshian Creek). Possibly in the Bay of Bengal subregion, in Diamond Harbour, and as far north in Farakka, India (Ishihara *et al.* 1998).

Comparisons. — This species is very similar to *H. gerrardi* Gray, *H. pastinacoides* Bleeker, and to two other unidentified species, tentatively named as *H.* sp. B (Arabian banded tail) and *H.* sp. C (Pakistan whipray). *Himantura* sp. D is distinguished from these species by a combination of characters, i.e. disc about as wide as long; denticles in band moderately sized to largish, squamation rate relatively fast; large midscapular denticle, square pearl-shaped; disc uniform light brown, plain, without any spotting; tail blackish, weakly banded dorsally (dark bands 2-7 times wider than white rings).

Remarks. — Of the 6 specimens identified herein as *H.* sp. D, four are from Pakistan (Sind and Karachi), and two are from the Bay of Bengal sub-region (i.e. Farakka, India and Chandpur, Bangladesh). The specimens, all on loan from various museums (i.e. The Natural History Museum of Los Angeles County, California Academy of Sciences, and the Museum of Tokyo University of Fisheries), were previously identified as *H. gerrardi.*

The assignment of the Indian and Bangladeshi specimens under this species heading is tentative however, pending additional specimens. Both have blackish tail with weak alternating bands, and slight marbled appearance beyond the sting especially on the ventral surface of the tail. The Indian specimen, figured in Ishihara *et.al.* (1998; note: disc width erroneously indicated as 676 mm; a measurement in year 2000 is 421 mm DW), resembles a large *H. pastinacoides*, except for its shorter tail, and weakly banded tail (morphometric ratios and meristics of *H.* sp. D and *H. pastinacoides* are slightly overlapping).

On the other hand, the species appear to fit the description of *Trygon ellioti* Blyth (1860), a species from India (Calcutta, Lower Bengal). This name is placed under the synonymy of *H. uarnak* by several workers (e.g. Garman 1913; Compagno & Roberts 1982), but is recognized by Eschmeyer (On-Line ver. February 15, 2002). Blyth described the species as having a plain uniform coloured disc, its tail with a slight marbled appearance beyond the sting but no distinct alternating band, and a central dorsal denticle band (not extended to sting) is developed at around 250 mm

DW. However, as it was described based partly on cut up specimens of both young and adult stages, with no designated type specimens, the name is herein considered as a *nomen nudum*.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

LACM 38130.047(1of3), LACM 38130.047(2of3), LACM 38130.047(3of3) (Sind, Pakistan); LACM 38131.043 (Karachi, Pakistan); MTUF 30005[?] (Farakka, India); CAS 141048[?] (Chandpur, Megna River, Bangladesh).

5.3 'UARNACOIDES' COMPLEX

5.3.1 Definition

Moderate to large species, adults exceeding 1 m in disc width. Disc shape suboval to subcircular; snout anteriorly truncated to acute at tip, moderately to extremely elongate; lateral apices broadly rounded (evenly rounded in *H. granulata*); tail stout, and whip-like, slightly depressed in cross-section at tail base and subcircular beyond sting base. Dorsal surface of disc generally with plain coloured (white specks often present in adult *H. granulata*); ventral surface often with a broad dark margins (blotched in adult *H. granulata*), sometimes uniform pale. Tail plain (uniform) coloured, upper half of dorsal surface darker than lower half. Teeth not sexually dimorphic, cusps of mature males not acute and elongate.

5.3.2 Key

1 Snout truncated infront of orbits; snout tip small, triangular, protruding prominently ... ... ***Himantura chaophraya* (p. 5-161)**

Snout not truncated infront of orbits **2**

2 Snout relatively short, preorbital snout length 20-30% disc width **3**

Snout moderate to extremely long, preorbital snout length 27-39% disc width ... **4**

3 Suprascapular denticle narrow heart-shaped, otherwise inconspicuous; denticles in secondary denticle band loosely-set, band margin not well-defined; trunk thick and raised at scapulocoracoid ... ... ***Himantura granulata* (p. 5-176)**

Suprascapular denticle ovate, prominent; denticles in secondary denticle band closely-set, band margin well-defined; trunk relatively thin, not raised at scapulocoracoid ... ... ***Himantura pastinacoides* (p. 5-188)**

4 Orbit relatively large, diameter less than 10 times in preorbital snout ... ... ***Himantura uarnacoides* (p. 5-205)**

Orbit smallish, diameter more than 10 times in preorbital snout **5**

5 Dorsal disc dark brown; oral moderately protrusible .. ***Himantura* sp. E (p. 5-220)**

Dorsal disc light grey; oral extremely protrusible... .. ***Himantura* sp. F (p. 5-231)**

Himantura chaophraya Monkolprasit & Roberts 1990

Giant freshwater whipray

Figures 3.2.1d, 3.2.6f, 3.2.7d, 3.2.8d, 3.2.9a, 3.2.10a, 3.2.11d, 5.3.1-5.3.2;

Tables 5.3.1-5.3.2

Himantura chaophraya Monkolprasit & Roberts 1990: 203 (original description based on three type specimens, holotype figured). Type specimens: KUMF 2998, 780 mm disc width, female (holotype); KUMF 2999, 1070 mm disc width, male (paratype); KUMF 3000, 192 mm disc width, female (paratype). Type localities: Thailand; holotype from Chao Phraya at Ayutthaya (about 100 km upriver from mouth of Chao Phraya into Gulf of Thailand); paratypes from Mae Nam Nan at Pichit (460 km upriver from Gulf of Thailand) (KUMF 2999), and Mae Nam Nan at Chumsang (60 km upriver from Nakorn Sawan and 360 km from Gulf of Thailand) (KUMF 3000).

Synonymy. —

Trygon polylepis Bleeker 1852: 73 (original description based on an immature male 310 mm disc width, not figured). Holotype: RMNH 7452, 301 mm disc width (measurement by P. Last). Type locality: Batavia (=Java), Indonesia.

Leiobatis (Himantura) polylepis: Bleeker 1877, pl. 558 (Plagiostom. Pl. 36), fig. 2 (illustration of holotype).

Urogymnus laevior Annandale 1909: 37 (original description based on a stuffed skin, complete with mouth and tail). Holotype: uncatalogued stuffed skin in the Indian Museum (Madras). Type locality: near shore at Malpe, south Canara on Malabar coast, India.

Trygon fluviatilis (not Hamilton-Buchanan): Annandale 1910: 2, pl. vi, fig. 1 (description based on at least two specimens; uncatalogued specimen with and without its tail in the Indian Museum, Madras). Locality: from off Madras coast between 20 and 30 fathom (36-54 m depth).

Himantura sp.: Compagno & Roberts 1982, 337, fig. 12 (undetermined immature male 210 or 284 mm total length, photograph of dorsal and ventral disc only). Locality: Lake Murray, Fly River basin, New Guinea.

Dasyatis fluviorum (not Ogilby): Merrick & Schmida 1984, 42 (misidentification).
Locality: Australia.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape subcircular; preorbital snout long, apical lobe distinct; anterior disc margin truncated; lateral apices broadly rounded. Dorsal surface of disc uniform light brown or greyish, ventrally white with broad dark brown marginal band, inner band margin with dark brown blotches; band beginning at apices of pectorals, continuing to free posterior tips of pectorals and pelvics, width on pelvics about half that of the pectoral; tail dark brown to blackish dorsally, ventrally white beginning tail base, becoming blackish from below sting base. Denticle band along mid-trunk moderately sparse, without well-defined margin, mid-scapular denticle small or inconspicuous; tertiary denticles present.

Description. — Disc subcircular, width 0.88-0-95 in length in specimens from Sabah, Ganges, and Chao Phraya (0.85-0.98 in two Australian specimens); moderately robust, center raised at mid-scapular, maximum disc thickness 0.08-0.14 (0.09-0.11) in disc width (DW); preorbital snout long, narrowly concave, with a distinct apical lobe, angle 112.0-117^{o} (120.5-121.5^{o}); anterior margins of disc truncated, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.3.1-5.3.2). Pelvic fins rather short, 13.4-20.5% (18.7-19.0%) DW; width across base 9.6-12.3% (11.3-12.2%) DW. Mature male specimen not available for examination of clasper structure; the following clasper description of a mature male of one of the paratypes (KUMF 2999; 107 cm DW) is based on Monkolprasit and Roberts (1990): claspers relatively massive 20.9 cm long and 4.6 cm wide near base; clasper groove 13.2 cm long, pseudosiphon aperture 2.1 cm long. Tail slender and whiplike, tapering gently toward sting, length 1.93-2.41 times disc width; base compressed, subcircular in cross-section, width 1.18-1.64 (1.30-1.40) times height at base.

Snout long, depressed; preoral snout length 3.75-4.34 (3.27-3.33) times mouth width, 2.78-3.22 (2.36-2.56) times internarial distance, 26.3-34.6% (27.5-28.2%)

DW; direct preorbital snout length 2.32-2.88 (1.55-1.70) times interorbital length, horizontal length 2.22-2.76 (1.50-1.63) times interorbital length; snout to maximum disc width 41.2-50.0% (34.3-41.6%) DW; interorbital space raised; eye small, diameter 27-38% (38%) spiracle length; orbits slightly protruded, diameter 0.49-0.61 (0.61-0.73) in spiracle length, interorbital distance 3.23-3.90 (3.78-4.72) times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils small, slightly laterally expanded, outer margin with a weak concavity, length 0.30-0.37 (0.28-0.29) in internasal distance; internasal distance 0.36-0.42 (0.49-0.52) of prenasal length, 2.69-3.34 (3.39-3.61) times nostril length. Nasal curtain subrectangular, broad, width 1.94-2.51 (2.07-2.28) times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth slightly arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 4-5 well-developed papillae; medial pair simple, rounded distally, longitudinally flattened, subequal in size and almost four times larger than outer pair, located near to each other; outer pair located at each corner of mouth, widely separated from inner pair; fifth unpaired papillae located between medial pair. Monkolprasit and Roberts (1990) noted 4-7 papillae, being 5 in holotype.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth rows 22-23 in upper jaw, 19-23 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.11-1.65 (1.33-1.50) times length of fifth, 0.33-0.41 (0.35-0.41) of mouth width; distance between first gill slits 1.86-2.07 (1.81-1.95) times internasal distance, 0.37-0.40 (0.41-0.42) of ventral head length; distance between fifth gill slits 1.37-1.57 (1.28-1.38) times internasal distance, 0.27-0.31 (0.29-0.30) in ventral head length.

Squamation. — Stages of squamation with overlapping size ranges, Stages 4 and 5 developing simultaneously; development of primary denticle band simultaneous with centre of disc appearing raised. Tail only sparsely covered with denticles except in very large adults (>1 m DW).

Holotype is in mid Stages 4 and 5: its entire dorsal surface including pelvic fins and tail, covered with fine rough denticles. Denticles on elevated central portion of disc, from just in front of eyes anteriorly and continuing onto base of tail posteriorly, distinctly larger than those on lateral portion of disc. Four slightly enlarged heart-shaped suprascapular denticles (5, 3, 2 and 3 mm in diameter) in a longitudinal row. A few slightly enlarged prickle-like denticles on mid-dorsal line of tail just anterior to sting. Tail anterior to sting with fine prickle-like tubercles dorsolaterally, ventral surface smooth. Tail posterior to sting uniformly covered with fine sharp denticles; half of sting has been broken off (Monkolprasit & Roberts 1990).

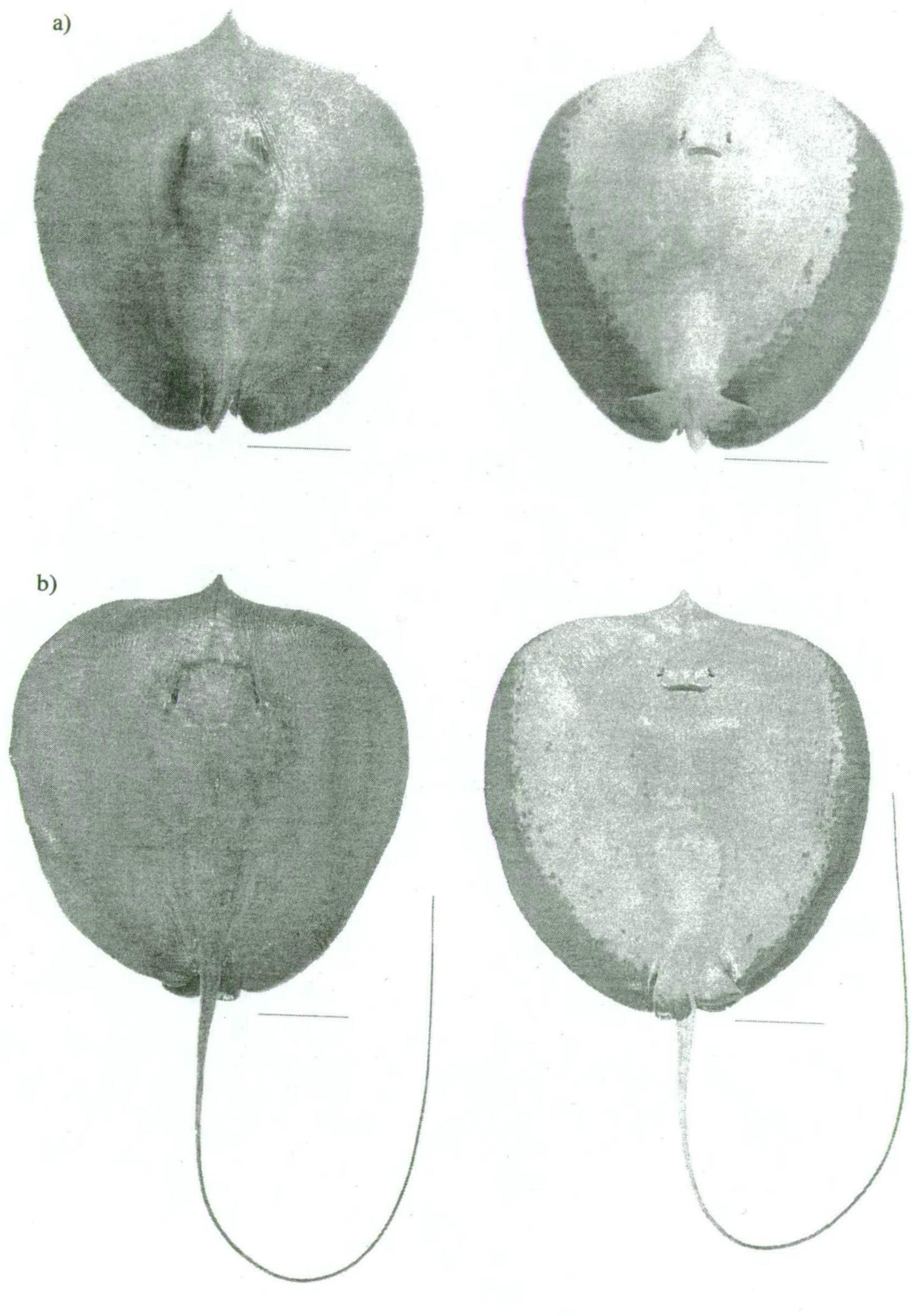
Stages 0, 4 and 5: from birth (ca. 300 mm DW) — Entire dorsal surface of disc covered with fine rough denticles. Secondary denticle band without well-defined margin. Denticles along trunk largest, gradually becoming smaller towards disc margin of secondary band; tertiary denticles uniform in size. Suprascapular denticle heart-shaped, its distal end pointed upwards; number varying from 1 to 6.

Stages 1, 2, 3 and 6 not applicable for this species.

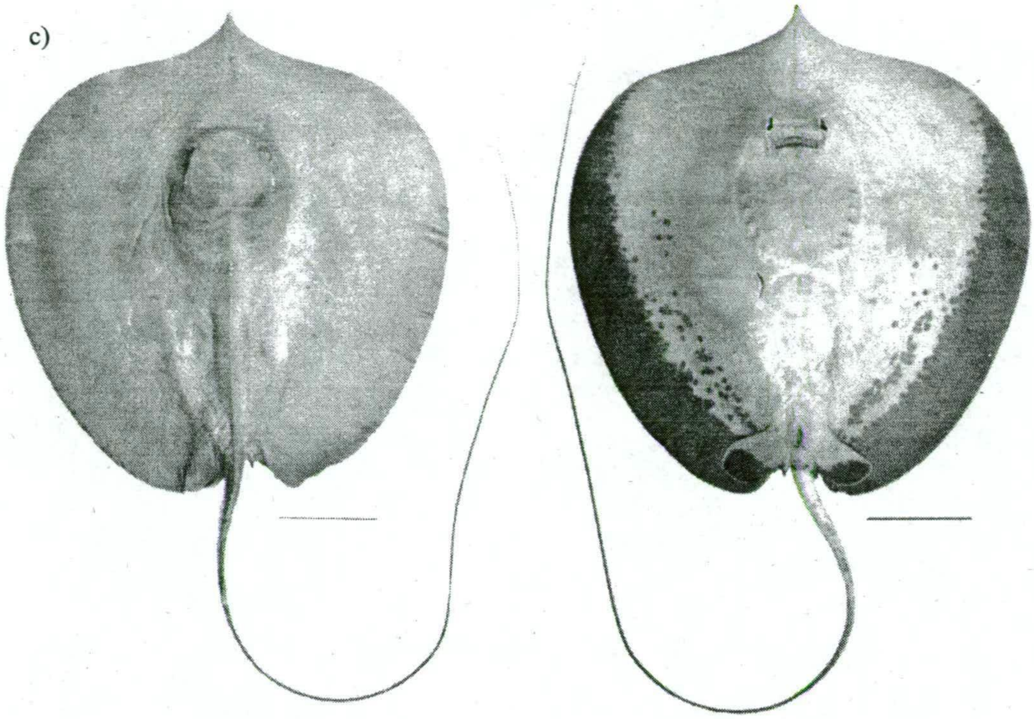
One to two elongated stinging spines; usually with one sting.

Meristics. — Total pectoral-fin radials 165-169 (n=4; Australian and Thailand specimens not radiographed); propterygium 67-73 (n=3), mesopterygium 32-36 (n=3), metapterygium 63-66 (n=3); pelvic-fin radials 24-27 (n=3); vertebral segments 108-112 (n=3), monospondylous 54-57, prespine diplospondylous 60-64, and postspine diplospondylous 0.

Figure 5.3.1. Representative specimens of *Himantura chaophraya* of similar disc size from various localities, in dorsal and ventral views. a, 363 mm DW (SMKK KTG7-21096; neonatal male; Kinabatangan River, Sabah, Malaysia); b, 430 mm DW (CSIRO H2524.01; female; Gilbert River, QLD, Australia ; photos by T. Carter); c, 450 mm DW (MTUF [India-5]; immature male; Bhagalpur, India); d, 460 mm DW (MTUF 30203; immature male; Chao Phraya River, Thailand). Bars 10 cm.



c)



d)

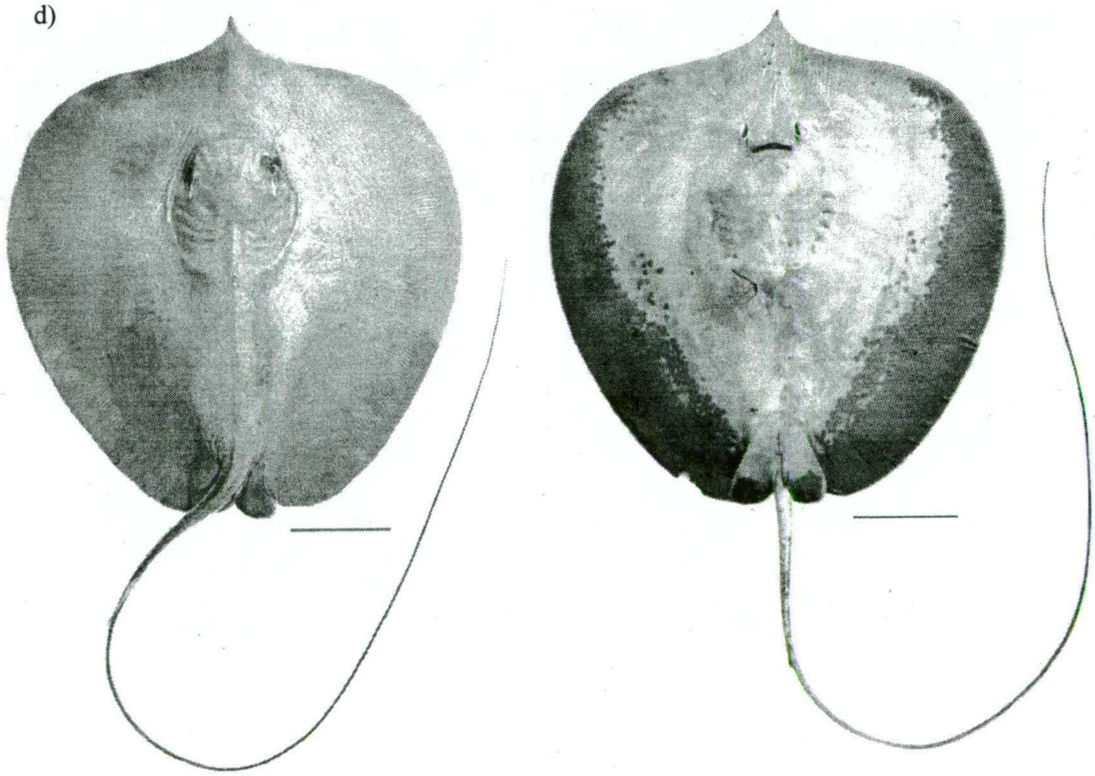
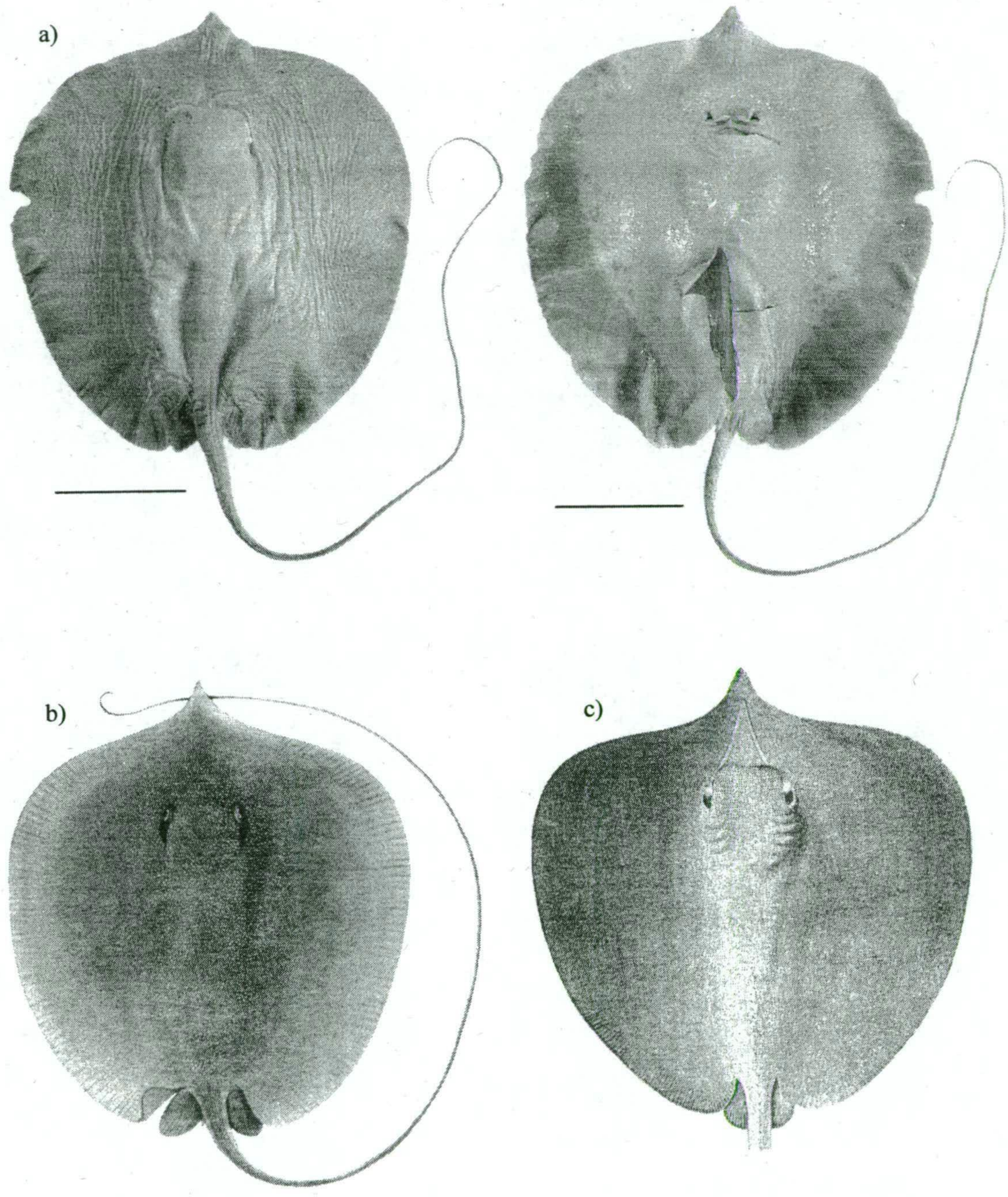


Figure 5.3.2. a, Holotype of *Trygon polylepis* (301 mm DW; RMNH 7452; immature male; Java Indonesia; photos and measurements by P. Last) in dorsal and ventral views; b, illustration of *Trygon polylepis* (310 mm DW in original description; reproduced from Bleeker 1877: fig. 2, pl. 558, Plagiostom. Pl. 36); c, illustration of *Trygon fluviatilis* (1390 mm DW; Madras coast, India; reproduced from Annandale 1910: pl. vi, fig. 1). Bars 10 cm.



a)
b)
c)

Colour. — In fresh, disc uniform light brown or greyish. Ventral disc white with broad dark brown marginal band, inner band margin with dark brown blotches; band beginning at apices of pectorals, continuing to free posterior tips of pectorals and pelvics, narrow anteriorly, becoming wider posteriorly, width on pelvics about half that of the pectoral. Tail dark brown to blackish dorsally; ventrally white beginning tail base, becoming blackish from below sting base.

Skeletal morphology. — Neurocranium of 372 mm DW immature male (Figs. 3.2.7d, 3.2.8d) with moderately elongate nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval; anteroposterior fontanelle keyhole-shaped, which extends to level of postorbital process insertion; efferent spiracular artery foramen below optic stalk on lateral surface of basal plate, midlength of cranium; preorbital processes short, knob-like; supraorbital crests concave along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commisure broad.

Scapulocoracoid (Fig. 3.2.10a) relatively broad, low, posterior part strongly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle low and short, 1.5 times as high as long; mesocondyle relatively short and broad, separated from metacondyle by deep notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11d) narrowly arched, relatively thick, median prepelvic process present, small anterolateral processes, moderately long dorsal iliac processes, and narrowly rounded mesial ischial processes.

Mixopterygium of adult males unknown.

Size. — Birth size around 300 mm DW (up to four pups per gestation period); length at first maturity (males) between 900 and 1300 mm DW. Three male specimens whose disc widths range between 500 and 620 mm, are all immatures (maturity stage 2). The male paratype with disc width 1070 mm (KUMF 2999), is mature (Monkolprasit & Roberts 1990). On the other hand, a slightly larger male, 1210 mm DW (SMKK SKN10-15697; only tail saved; colour print courtesy of S. Mycock and R. Cavanagh), is reported as an adolescent (maturity stage 3). Females probably mature around 800 mm DW (L. Squire, pers. comm. with P. Last, Jun 2001), reaching to 2 m DW (one of the paratypes, KUMF 3000, has a disc width of 1920 mm).

Etymology. — Not specified, but apparently after the Mae Nam Chao Phraya in Thailand, where the holotype was obtained about 100 km upriver from its mouth into the Gulf of Thailand.

Common name. — Giant freshwater whipray (Monkolprasit & Roberts 1990).

Distribution. — Reported from India (Malabar coast; Ganges River; Orissa), Thailand (Mae Nam Chao Phraya, Mae Nam Nan), Bangladesh, Laos, Malaysia (Kahang River of the Endau basin, Johore; Kinabatangan and Padas Rivers, Sabah), Indonesia (Java; Mahakam Basin), tropical Australia, Papua New Guinea (Fly River Basin) (e.g. Compagno & Roberts 1982; Monkolprasit & Roberts 1990; Last & Stevens 1994; Tanaka 1998a; Anon 1999; Fowler *et. al.* 1999).

Comparisons. — This species belongs to the large ray group, whose size at birth is around the maximum size of the dwarf ray group (i.e. 'signifer' complex; this study), and whose disc widths easily exceed 1000 mm. Following is a comparison between specimens of *H.* cf. *chaophraya* from various localities in the Indo-Pacific.

The Kinabatangan specimens (e.g. Fig. 5.3.1a), including large ones from both east and west coast Sabah rather look more similar to the holotype of *T. polylepis* Bleeker (Fig. 5.3.2a), although Bleekers (1877) own illustration of the species (Fig. 5.3.2b) appear different, resembling more like *H. granulata* (Macleay). The snout tip is more triangular, and anterior disc not as truncated but rather more convex, compared with Thai and Australian specimens (Figs. 5.3.1b-d).

Analyses of morphometric and meristic data of Australian, Indian, Malaysian (Sabah), Thai and Indonesian specimens (see 'Materials'), which include specimens collected from fresh and brackish water localities, revealed that while there are indeed several differences in the morphometric ratios, particularly in snout-head measurements between Asian and Australian specimens (Tabs. 5.3.1-5.3.2), meristic counts are more or less overlapping (see also Taniuchi *et. al.* 1991). The preoral snout length of Australian specimens averaged around 28% DW, whilst Asian specimens (including the types) averaged slightly longer, i.e. 31-32% DW (29.7% DW in holotype, Monkolprasit & Roberts 1990).

All of the rays examined however, differ from the types of *H. chaophraya* as described by Monkolprasit and Roberts, by the absence of denticles on the dorsal surface of the pelvic fins (i.e. dorsal surface smooth).

There also appear to be slight variations in shape and number of suprascapular denticles even among specimens from the same locality. However, different squamation pattern (i.e. presence or absence of stellate denticle pattern) between specimens from different localities (i.e. between Kinabatangan and Australian specimens in particular) (J. Caira and K. Jensen pers. comm. Jul 2002; pers. observation), further support these different forms as different species. These stellate patterns resemble that illustrated in James (1980: fig. 1b), of a specimen identified as *H. marginata* (see also remarks under species heading of *H. marginata*).

Remarks. — *Himantura chaophraya* is the most recently described Indo-Pacific stingray species, with all three types each reported from three different freshwater (i.e. at least a hundred kilometres from the sea) localities in Thailand. The authors however, did not exclude the possibility of the species occuring in the sea (Gulf of Thailand), suggesting more intensive marine field surveys, while cautioning that the lack of report (particularly in newspapers) of the species from marine habitat, is likely because many other large stingrays and other elasmobranchs occur there, thus its presence there is not something newsworthy.

Following Monkolprasit and Roberts' description, the species have been reported from elsewhere within the region. In 1991, Taniuchi *et. al.* reported the first record from Australia. Later, Last and Stevens (1994) reported the species as the only Australian stingray to live only in fresh and estuarine waters, and attributed the lack of previous reports as due to misidentification as other species.

In 1996, the species was recorded from two major rivers, and a coastal (Sandakan) fish market in Sabah (Malaysia) (Fowler *et. al.* 1999; Manjaji 2002a, b). Apparently, locals living along the rivers, have long known about the existence of large freshwater stingrays and other riverine elasmobranchs (Fowler & Payne 1995). The only specimen observed at the fish market is rather more likely caught from waters from adjacent coastal shores rather than from a distant freshwater locality along major rivers nearby (see also Manjaji 2002b).

Between 1996 and 1998, the species was recorded from rivers in several mainland Asian countries during field surveys dedicated to freshwater elasmobranch research organised by a team of Japanese researchers (Tanaka 1998a, b). Several of the specimens obtained from these surveys now deposited in the Museum of Fisheries Sciences, Tokyo University of Fisheries (MTUF) were examined (by myself) in 2000, and tissue samples from frozen specimens taken for DNA analysis (H. Ishihara and S. Tanaka pers. comm.).

More recently, are anecdotal reports of specimens resembling the species from Johore (Peninsula Malaysia), and Orissa (India). According to K. Lim (pers. comm. 1999), the Johore record although reported as marine fish (Anon 1999), is rather more likely caught from the tidal reaches of Kahang River of the Endau basin. The Orissa record, firstly reported in several Indian newspapers in 2001, although is a large specimen (600 mm DW, female), apparently lacks dorsal disc squamation, and the diagnostic broad dark brown marginal band on the ventral disc surface (B. Mohanty pers. comm. Nov 2001).

Lyle Squire (pers. comm. with P. Last, Jun 2001) on the other hand, observed a direct correlation between bottom types and the spots in Australian specimens caught from freshwater habitats near Kurumba (northern Australia).

In their work, Last and Stevens (1994) remarked that the Australian rays appeared to be smaller than those reported from Asian rivers (see also Last 2002). Leonard Compagno (pers. comm. 1997) further suggested that it is possible that more than one species of these large plain whiprays exist, and that the marine or euryhaline form or forms may be different from the freshwater forms. These forms are tentatively treated as members of the '*Himantura fluviatilis*' complex (Compagno & Cook 1995; Compagno 2002).

Roberts (1998; pers. comm.) too, believed there are more than one species of the large ray group, and noted that the Kinabatangan River specimens (collected in 1996) are not conspecific with the Thai species, citing differences in disc shape. However, he argued that only one name is available for a species of the large ray (i.e. *H. chaophraya* Monkolprasit & Roberts), and that past and present use of the name *Himantura fluviatilis* (Hamilton-Buchanan 1822) is based on unwarranted assumptions.

He (T. Roberts pers. comm. 1998) noted the disc shape of small and large size specimens of *H. chaophraya* from the Chaophraya River is the same, and that a juvenile specimen from the Kinabatangan River appeared to have a different disc shape.

Molecular analyses (16S, cytochrome *b*) of samples from Thai, Malaysian (Padas and Kinabatangan Rivers in Sabah), and Australian specimens lend support to the above hypotheses, with representatives from the different areas clustering together. However, the trees are only supported by low bootstrap values (see also 'Discussions' in Chapter 4, figs. 4.2.11-4.2.12; Sezaki *et. al.* 1999).

On synonymy, *Trygon polylepis* Bleeker, described based on a young specimen from Indonesia, is a possible name for Borneo representatives (see 'Comparisons'), but is tentatively treated as a senior synonym of *H. chaophraya*.

The nominal taxon *Raja obtusa* Ehrenberg in Klunzinger 1871, described from the Red Sea, and mentioned in the synonymy of *T. polylepis* Bleeker, could not be verified, as the paper was not available despite several attempts to obtain it. It is herein tentatively treated as a *nomen nudum* (see also Eschmeyer On-Line Version, Updated February 15, 2000).

A new synonym added to the list of synonym is *Urogymnus laevior* Annandale 1909. The holotype, a dry specimen hanging on a wall in the Indian Museum, was briefly observed (P. Last pers. comm. 2000) as having a similar disc shape as *H. chaophraya*. Pending more data on the specimen, the name may be available for the large ray species from India, and is also tentatively treated as a senior synonym of *H. chaophraya*.

Comments on the type status of other specimens listed by Eschmeyer (On-Line Version, Updated February 15, 2000), is not possible as these were not examined during this study.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CSIRO H2503.01[a] (Pentecost River, WA, Australia); CSIRO H2524.01 (Gilbert River, QLD, Australia); CSIRO H5283.01[a], SMKK KTG2-23397, SMKK KTG3-20497, SMKK KTG7-21096, UMS MMKG1 (Kinabatangan River, Sabah, Malaysia); MTUF 30233 (Rajmehar, India); MTUF 30203[e] (Bhagalpur, India); MTUF 30204[e], MTUF 30205, MTUF 30206 (Chao Phraya River, Thailand); RMNH 3365[c] (unspecified locality); RMNH-T 7452[c] (holotype of *Trygon polylepis*) (Java, Indonesia); SMKK BFT1-697[e] (Padas River, Sabah, Malaysia); SMKK SKN10-15697[e] (Sandakan, Sabah, Malaysia).

Himantura granulata (Macleay 1883)

Whitetail whipray

Figures 3.2.5d, 3.2.7a, 3.2.8a, 3.2.9b, 3.2.10w, 3.2.11g, 3.2.12b, 5.3.3;

Tables 5.3.3-5.3.4

Trygon granulata Macleay 1883: 598 (original description based on a specimen 13 inches disc diameter, approximately 330 mm disc width, not figured, no designated types, but see Whitley [1928]). Type specimens: AMS I9763, 331 mm disc width, female (holotype); AMS 1A.2867, 292 mm disc width, male (allotype). Type locality: 9° 29'S, 147° 5'E, Port Moresby District, Papua New Guinea (holotype); from reef off Sunday River, Vanikoro (allotype).

Synonymy. —

Himantura granulata: Jordan & Seale 1906, 185 (listed).

Trygon ponapensis Günther 1910: 493, taf. 180 (original description based on a young specimen, illustrated). Holotype: BMNH 1879.5.22.105, 163 mm disc width (184 mm disc width, measurement by P. Last), neonatal female. Type locality: Kubary, Ponapé.

Dasybatus (Himanturus) ponapensis: Garman 1913, 380 (description after Günther).

Dasyatis ponapensis: Fowler 1928, 24 (brief description).

Dasyatis granulatus: Fowler 1931, 314 (listed). Locality: Oceania (=eastern region of tropical Pacific).

Dasyatis (Amphotistius) ponapensis: Fowler 1941, 432 (description after Günther). Locality: Micronesia.

Dasyatis (Amphotistius) granulatus: Fowler 1941, 437 (description after Whitley's [1928] redescription). Locality: East Indies and Melanesia.

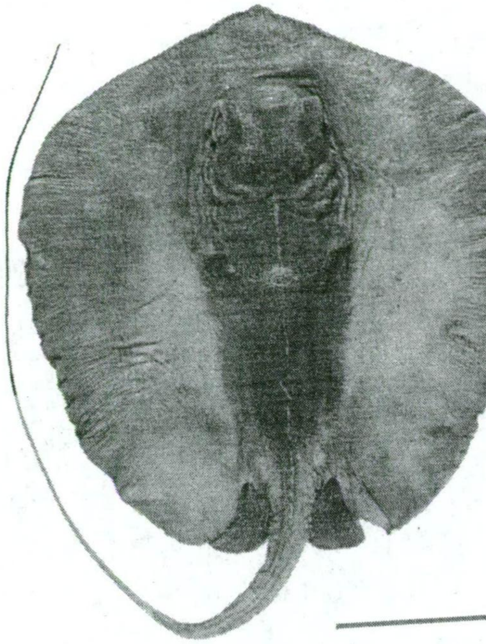
Himantura marginatus (not Blyth): James 1980, 161 (description based on two mature male specimens, misidentification in part). Locality: Gulf of Mannar near Mandapam (the gulf is an arm of the Indian Ocean extending east to west between India and Sri Lanka at a width of 160 to 200 km).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape oval, strongly robust, disc raised along trunk. Orbits strongly protruded even in large mature specimens. Dorsal surface of disc blackish, peppered with small white spots of size more or less of the pupil, over entire disc including pelvics and tail pre-sting; thick mucous enveloping outer layer of dorsal surface when removed, reveals light yellowish brownish surface beneath blackish colouration; ventrally uniform pale in young; densely blotched with black spots in larger specimens and adults; tail entirely white after sting. Disc void of denticles at birth until about 230 mm DW; developed secondary denticle band with well-defined margin, denticles in band conical, abutted, midscapular denticle small or inconspicuous; tertiary denticles minute granulous.

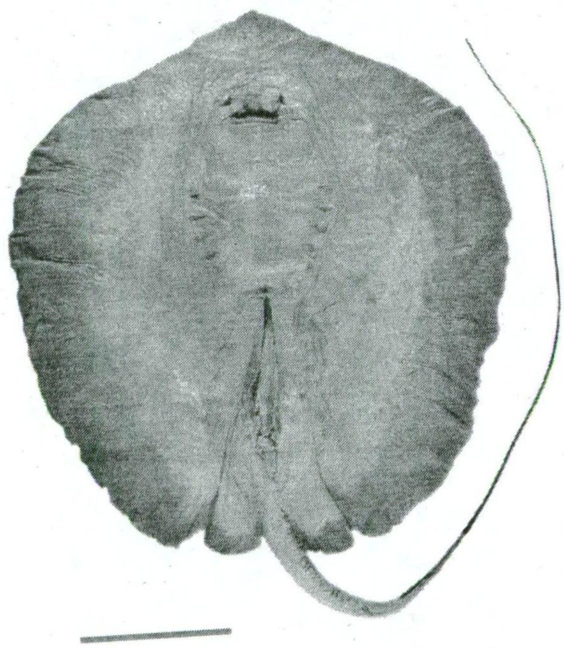
Description. — Disc oval, width 0.93 (0.90-0.98) in length; strongly robust, disc raised along trunk, above the pectorals, maximum disc thickness 0.11 (0.13-0.23) in disc width (DW); preorbital snout short not produced, broadly convex, apical lobe fine pointed, angle 123^{o} (122-133^{o}); anterior margins of disc strongly convex, lateral apices evenly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.3.3). Pelvic fins moderately long, rectangular, posteriorly broadly rounded, 22.8% (18.3-24.0%) DW; width across base 13.3% (11.6-16.3%) DW; free rear tip extending slightly past free posterior tip of pectoral-fin. Claspers of adult male (Fig. 3.2.5d) long and stout, rod-like, even width from base to tip, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge slightly concave; lining of pseudopera smooth; hypopyle short, less than 1/3rd of clasper length on its outer margin, prominent notch anteriorly. Tail broad-based, whiplike, tapering gently toward sting (tip damaged in holotype), length 1.26-2.05 times disc width; base depressed, subcircular in cross-section, width 1.78 (1.06-1.55) times height at base. Tail of holotype with two shallow longitudinal grooves running parallel to each other along ventral surface from below sting base.

Figure 5.3.3. Holotype of *Himantura granulata* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of oronasal (nostrils and nasal curtain distorted). AMS I9763 (331 mm DW; female; Port Moresby District, Papua New Guinea). Photos by T. Carter. Bars 10 cm.

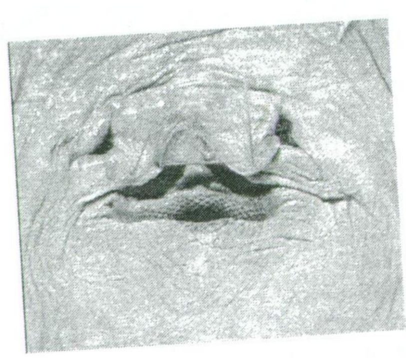
a)



b)



c)



Snout short, obtuse, depressed; preoral snout length 3.00 (2.42-3.26) times mouth width, 2.49 (1.80-2.60) times internarial distance, 24.1% (19.9-26.0%) DW; direct preorbital snout length 1.71 (1.25-2.00) times interorbital length, horizontal length 1.64 (1.19-1.60) times interorbital length; snout to maximum disc width 41.7% (42.2-51.5%) DW; interorbital slightly concave; eye moderately large, diameter 69% (39-76%) spiracle length; orbits strongly protruded, diameter 1.20 (0.57-1.09) in spiracle length, interorbital distance 1.59 (1.34-2.76) times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally; spiracular margin of young lobe-like in dorsal view. Nostrils moderately large, narrow, laterally expanded, outer margin with a weak double concavity, length 0.37 (0.42-0.58) in internasal distance; internasal distance 0.52 (0.51-0.75) of prenasal length, 2.71 (1.73-2.39) times nostril length. Nasal curtain skirt-shaped, posteriorly expanded, relatively broad, width 2.09 (1.74-2.14) times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; moderately deep curved groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about more than half mouth width apart; lips well-corrugated, especially skin on lower jaw, not confined to narrow strip around lips; enlarged sensory pores on chin readily visible in large specimens (ca. 800 mm DW). Mouth floor with 2-7 well-developed papillae, the number and arrangement variable; holotype with medial pair distally fimbriate, distally rounded to fimbriate in others; medial papillae (2-3) enlarged, longitudinally flattened, subequal in size, located near to each other; outer papillae located at each corner of mouth, widely separated from inner pair. Palate with single central longitudinal ridge of skin, surface weakly papillose.

Teeth small, about 1.5 mm in width, smaller in upper jaws; closely-set, crowns well separated from one another; size slightly varying continuously lateral to symphysis, largest at or adjacent symphysis, smallest near mouth corner appearing somewhat sharp; lozenge-shaped with a cusp over its long axis (Whitley 1928); tooth rows 20 (23) in upper jaw, 25 (21-26) in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.28 (1.23-1.59) times length of fifth, 0.43 (0.43-0.55) of mouth width; distance between first gill slits 2.29 (1.88-2.61) times internasal distance, 0.42 (0.41-0.48) of ventral head length; distance between fifth gill slits 1.51 (1.25-1.85) times internasal distance, 0.28 (0.28-0.34) in ventral head length.

Squamation. — Stages of squamation with narrow size ranges. Rate of squamation relatively slow, disc void of denticles at 235 mm DW; suprascapular denticle small or inconspicuous.

Holotype is in mid Stage 4 (Fig. 5.3.3): its dorsal surface with a subrectangular denticle band; margins of denticle band along trunk well-defined; suprascapular denticle small or inconspicuous; denticles on snout minute blunt conical with wide round base, becoming narrow conical around orbit-spiracular area; interorbital and on trunk, denticles larger, varying in size and shape (blunt conical to blunt rod with flat stellate base), sparsely arranged with about 1-2 denticles apart; from tail base to sting base, denticles with hook-like crowns, base flat round to stellate arranged in a row; ventral and lateral surfaces of tail void of denticles.

Stage 0: from birth (ca. 140 mm DW) — Disc entirely smooth; suprascapular denticle not developed at this stage, may appear later.

Stage 4: (ca. 230 mm DW) — Denticles simultaneously appearing along trunk and tail, not forming separate patches; without evidence of primary denticle band; denticles on disc sparsely distributed, arranged in a single row on tail; denticles blunt conical with round flat base.

As the development progresses, more denticles appearing but remain widely spaced. Denticle band forming a rectangular shape above scapular region; anteriorly extending a short distance in front of orbits, posteriorly decreasing towards tail base continuing weakly onto tail until sting base; band margin weakly defined.

In late part of the stage, secondary median denticle band developed as a continuous, subrectangular longitudinal band with well-defined margins; denticles fully exposed, becoming abutted; largest along trunk, laterally decreasing in size; interorbital and interspiracular area most densely covered with denticles; most closely set on head region. On snout, narrow spinulous conical denticles with wide round base appearing, base embedded in skin; interorbitally, denticles wide spinulous conical with flat round base; scapular with conical and heart-shaped denticles interspersed, heart-shaped denticles with raised, vertical crowns and convex base; above abdomen, denticles conical with convex base, some with two crown peaks and stellate base; conical denticles continue narrowly along dorsal tail base to almost length of tail, becoming hooked-like with its base spread and minute behind sting.

Stage 5 (ca. 300-350 mm DW) — Denticles distributed over entire dorsal surface of disc, sub-equally spaced including those outside of the trunk area, although most dense along trunk; size significantly smaller (minute) on lateral margin, it appears as if the denticles are confined to the trunk area.

Two narrow heart-shaped suprascapular denticles present in one specimen; crown slightly concave, with extremely convex exposed base.

Stages 1, 3 and 6 not applicable for this species.

One sting present at birth; blunt sting tip emerging from surface of dorsal tail; second sting may emerge above first sting at around 320 mm DW. Sting large, width as wide as tail from which the sting base originated; still covered under skin especially around the edges and tip, in specimens of up to 330 mm DW.

Meristics. — Total pectoral-fin radials 145-146 (142-148; n=4); propterygium 64 (63-67), mesopterygium 18-20 (14-21), metapterygium 62-63 (61-68); pelvic-fin radials 33 (23-33; n=5); vertebral segments 143 (136-144; n=2), monospondylous 51 (48-52) (n=8), prespine diplospondylous 92 (86-93) (n=5) and postspine diplospondylous 0 (0-3) (n=4). Of the specimens radiographed, three had 2-3 postspine diplospondylous vertebrae, while the rest of the specimens had the vertebrae ending just before the sting base.

Colour. — Dorsal surface of holotype almost uniformly dark reddish brown with paler abraded areas (presumably through handling and preservation), dark dendritic markings of the sensory pore opening along the disc margin; disc margins not paler in colour, no evidence of spotting; ventral surface paler, with evidence of broad dark margins even on pelvics, and dark blotches on inner disc margin surface; oronasal area plain pale; tail not banded, displaying paler colouration beyond sting.

In fresh, dorsal surface of disc blackish, peppered with small white spots of size more or less of the pupil, over entire disc including pelvics and tail pre-sting; tail entirely white after sting; thick mucous enveloping outer layer of dorsal surface when removed, reveals light yellowish-brownish surface beneath blackish colouration. Ventral surface uniform pale in young; densely blotched with black spots in larger specimens and adults, variably sized and light and heavy tones of black spots scattered over entire ventral surface, particularly along disc edge. Ventral surface entirely black in a relatively small specimen from the Philippines.

Young preserved specimens up to 350 mm DW, uniform light to dark grey dorsally, without any spotting except for dark dendritic markings of the sensory pore opening; markings arranged around inner margin of disc in a uniform row conforming to disc shape; tail evidently pale in colour.

Skeletal morphology. — Neurocranium of 276 mm DW immature male (Figs. 3.2.7a, 3.2.8a) with elongate nasal capsules, anterior edge broadly rounded, slightly concave medially; nasal apertures transversely rectangular; distinctive keyhole-shaped anteroposterior fontanelle, which extends to level of postorbital process insertion; efferent spiracular artery foramen just ahead below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes short but robust, triangular, posteriorly bluntly pointed; supraorbital crests low and strong, slightly concave along orbital margin;

pseudo orbital fissure present in orbital region; sphenopterotic ridge a narrow ledge with straight margins; lateral commisure broad.

Scapulocoracoid (Fig. 3.2.10w) relatively narrow, moderately high, posterior part short, weakly extended in lateral view; lateral face subrectangular, with narrow base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle relatively low and moderately long, 2.5 times as high as long; mesocondyle rounded, separated from metacondyle by deep notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11g) narrowly arched, relatively thick, median prepelvic process present, small anterolateral processes, moderately long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium (Fig. 3.2.12b) relatively simple; structure of basal segments unknown (clasper specimen was cut halfway along the axial); beta cartilage present as a separate element, merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, paddle-shaped, posterior edge merging with dorsal terminal cartilage, medial flange broad, lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, oval subrectangular, and scoop-shaped; terminal tip of axial cartilage short, spatula-like; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, and narrowly extending to inner lateral surface.

Size. — Birth size around 140 mm DW; length at first maturity (males) between 550 and 650 mm DW. A 520 mm DW male specimen (BPBM 34745) is reportedly immature (Ishihara *et al.* 1993), while two others (MTUF 26703 and MTUF 26719) 686 and 687 mm DW respectively, as mature (maturity stage 4). Females reaching to 780 mm DW, as based on a specimen (MTUF 26700) from Micronesia.

Etymology. — Not specified, but the epithet *granulata* is probably based on the granulous dorsal disc surface of this species.

Common names. — Mangrove ray (Whitley 1940; Marshall 1966); Macleays coachwhip ray (Whitley 1940); Whitetail stingray (Ishihara *et al.* 1993); Mangrove whipray (Last & Stevens 1994).

Distribution. — Widely reported from island nations in the eastern tropical Pacific region, (i.e. Papua New Guinea, Vanikoro, Ponapé, Melanesia, Philippines), also from western Indian Ocean (Gulf of Mannar, Sri Lanka), and South China Sea (Malaysia) (e.g. Marshall 1966; Debelius 1993; Homma *et al.* 1994; Johnson 1999; Compagno in Randall & Lim 2000).

This species appear to prefer rough rocky bottoms, although widely reported as found in mangrove area. They probably inhabit coastal areas with mangrove vegetation to coral reef areas in waters from the inner continental shelf, right throughout the Indo-West Pacific (Indian Ocean, South China Sea and pockets of seas in the western Pacific Ocean).

Comparisons. — This species belongs to the large ray group; size at birth relatively small, ca. 140 mm DW, and disc width apparently not exceeding 1 m.

This species shares similar disc shape (i.e. oval) and tail colour (i.e. entirely white after sting) with *H. signifer* (a member of the 'signifer' complex, consisting small-sized species; this study), which otherwise do not share any other characteristics.

On squamation, the denticle band margin is well defined when young, becoming weakly defined in large adults; denticles are widely spaced, lacking independent row of enlarged denticles along the midline of the tail. The sting is notably relatively enlarged and long, even in young, sting width as wide as tail width underneath the sting.

Remarks. — This species has been redescribed twice before, first in 1928 by Whitley, then in 1993 by Ishihara *et al.*. Whitley designated two type specimens, a female holotype and a male allotype, claiming the holotype was that used by Macleay to describe the species, and redescribed the species based on these designated types. Ishihara *et al.* redescribed the species based on six large adult specimens they obtained from reef areas of the Maldive Islands. It is noted that in both redescriptions, there was no mention of the ontogenetic pattern of colouration (see section on 'Colour').

On synonymy, *Trygon ponapensis* Günther 1910 is treated as a senior synonym of this species, where earlier researchers have either recognized it, or otherwise erroneously synonymized it with other species. Two most notable cases are discussed below. Günther only briefly described the species based on a young juvenile specimen whose disc is entirely naked. He however, provided a useful illustration depicting the disc shape from dorsal view, and oronasal area on the ventral surface. Data of the holotype (of *T. ponapensis*) is based on observations, including measurements and photographs by P. Last (pers. comm.)

Garman (1913) recognized *T. ponapensis*, but treated *H. granulata* (Macleay) as a synonym of *Himantura gerrardi* (Gray), for reasons remaining unclear. It may be possible however, that it did not cross upon him to compare the two, as is evident by his only reference to the comparison made in the original description, that *T. ponapensis* is close to another species. Fowler (1941) too, recognized *T. ponapensis* (based on Whitleys redescription), but placed it under a different genus and sub-genus *Dasyatis (Amphotistius)*, using the subgenera complexes proposed by Garman.

Himantura marginatus (Blyth 1960), a doubtful species, and thus treated as *incertae sedis* in this study (see also remarks under species heading of *H. marginata*), appears to be a closely related species, by description of the squamation. However, as described by Blyth, the denticles apparently extend to the entire ventral surface, particularly on the disc margin and around the gill openings, suggesting it as from another ray group (i.e. a skate).

The specimens identified as *H. marginatus* by James (1980) are decidedly *H. granulata*. James seemed to realize that his two adult specimens were lacking denticles on the ventral surface, as well as several other characteristics not conforming to the species, but nevertheless identified them as *H. marginatus*. He pointed out the disc shape of this species is as implied in Blyths original description, i.e. 'longer than wide' (rather than otherwise). Furthermore, he explicitly stated that the presence of characteristic stellate denticles along the trunk and the prickly nature of the tail, as the basis for identifying with *H. marginatus*. The photographs of one of the specimen, as well as proportional measurements and count range, clearly indicates these are *H. granulata* (James 1980: pls. I & II).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

AMS I9763 (holotype) (New Guinea); BMNH 1879.5.22.105[c] (holotype of *Trygon ponapensis*) (Kubary, Ponapé); CAS 52032 (Palau); CSIRO CA1255 (N of Anson Bay, WA, Australia); CSIRO H962.1, NTM S.10718.062 (NT, Australia); CSIRO H2751.01 (Groote Eylandt, NT, Australia); CSIRO H3864.01 (E of Cape York Peninsula, QLD, Australia); CSIRO H4417.01 (NE of Shelburne Bay, QLD, Australia); CSIRO H4426.32[a] (Java, Indonesia); MTUF 26700, MTUF 26703, MTUF 26719, MTUF 26903[e], MTUF 26906 (Micronesia); QM I5879, QM I20184 (QLD, Australia); SMF 4747[d] (Maldives); SUML JPAG207 (Philippines).

Himantura pastinacoides (Bleeker 1852)

Round whipray

Figures 3.2.4d, 3.2.5g, 3.2.6k, 3.2.7j, 3.2.8j, 3.2.10g, 3.2.11j, 3.2.12f, 5.3.4-5.3.7; Tables 5.3.5-5.3.6

Trygon pastinacoïdes Bleeker 1852: 75 (original description based on a single specimen, not figured). Holotype: BMNH 1867.11.28.161, 155 mm disc width, female. Type locality: Batavia (=Java), Indonesia.

Synonymy. —

Trygon pareh Bleeker 1852: 71 (original description based on a single specimen). Holotype: BMNH 1867.11.28.155, 436 mm disc width, female. Type locality: Batavia.

Leiobatis (Himantura) pareh: Bleeker 1877, fig. 2, pl. 557, Plagiostom. Pl. 35 (illustration of female holotype).

Leiobatis (Himantura) pastinacoides: Bleeker 1877, fig. 2a, pl. 559, Plagiostom. Pl. 37 (illustration of female holotype).

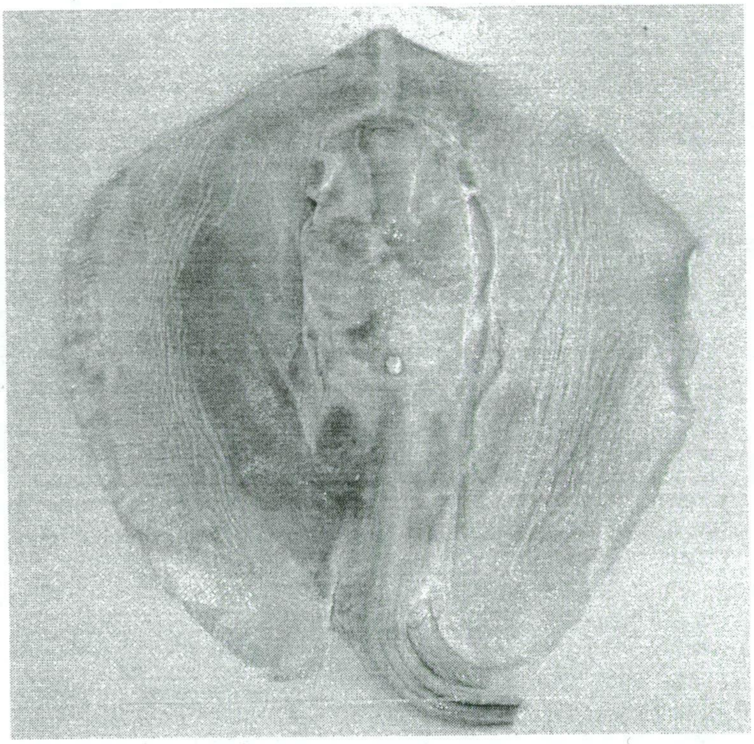
Himantura pastinacoides: Fowler *et al.* 1999, 262 (listed). Locality: coastal Sabah, Malaysia.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape suboval, robust, center raised at mid-scapular, preorbital snout moderately long, weakly convex, with a distinct apical lobe, anterior disc margin weakly convex, lateral apices broadly rounded. Dorsal surface of disc uniform dark brown to brownish green; ventral surface uniform pale sometimes with narrow light brown margins, ventral pelvic fins plain pale, light brown blotch on free posterior tip; tail dark brown, darker on dorsal half, whitish on ventral half from tail base to sting base. Disc with quite well developed secondary denticle band by 230 mm DW, more or less well developed by 300 mm DW; with a prominent ovoid suprascapular denticle.

Description. — Disc suboval, axis of greatest width almost equal to distance from tip of snout to pectoral-fin insertion, width 1.00 (0.95-1.06) times length; robust, center raised at mid-scapular, maximum disc thickness 0.11 (0.11-0.14) in disc width (DW); preorbital snout moderately long, weakly convex, with a distinct apical lobe, angle 127° (117-125°); anterior margins of disc weakly convex, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.3.4-5.3.7). Pelvic fins moderately long, 22.6% (16.4-22.6%) DW; width across base 15.7% (12.6-15.7%) DW. Claspers of adult male (Fig. 3.2.5g) long and stout, dorsal surface slightly convex, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, weak notch anteriorly. Tail broad-based, whiplike, tapering gently toward sting (tail of holotype damaged), length 2.20-3.04 times disc width; base depressed, subcircular in cross-section, width 1.47 (1.28-1.96) times height at base.

Snout moderately long, depressed; preoral snout length 2.81 (2.96-4.81) times mouth width, 3.02 (2.74-3.35) times internarial distance, 24.8% (21.2-30.2%) DW; direct preorbital snout length 1.61 (1.51-2.26) times interorbital length, horizontal length 1.47 (1.37-2.18) times interorbital length; snout to maximum disc width 39.8% (35.1-43.9%) DW; interorbital space flat; eye moderately large, diameter 59% (31-68%) spiracle length; orbits protruded, diameter 0.79 (0.50-1.08) in spiracle length, interorbital distance 2.23 (1.65-4.14) times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils large, slit-like, outer margin with a weak double concavity, length 0.38 (0.48-0.61) in internasal distance; internasal distance 0.45 (0.39-0.49) of prenasal length, 2.60 (1.64-2.13) times nostril length. Nasal curtain skirt-shaped, relatively broad, width 1.82 (1.56-2.30) times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, weakly concave to weakly double concave.

Figure 5.3.4. Holotype of *Himantura pastinacoides* in dorsal and ventral views. BMNH 1867.11.28.161 (155 mm DW; female; 'East Indies'). Photos and measurements by P. Last. Bars 10 cm.



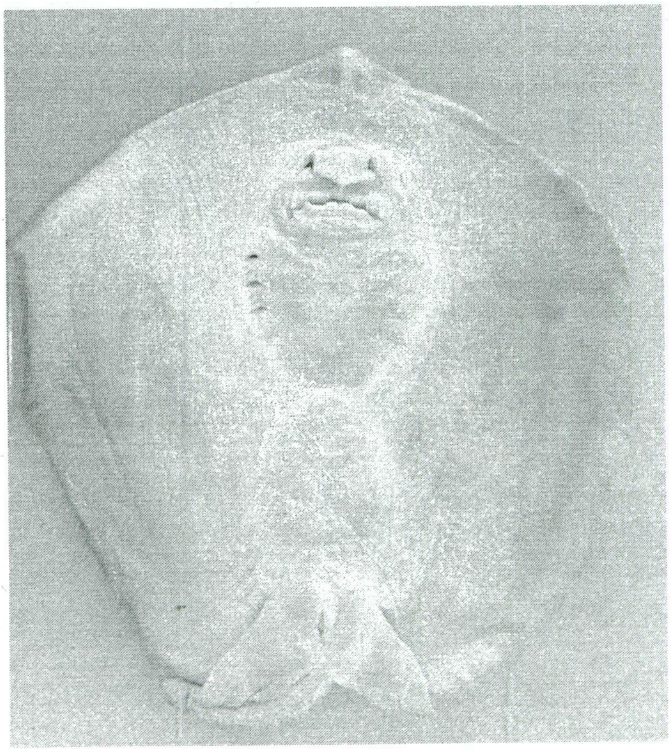


Figure 5.3.5. Illustration of *Himantura pastinacoides* (reproduced from Bleeker 1877: fig. 2a, pl. 559, Plagiostom. Pl. 37).

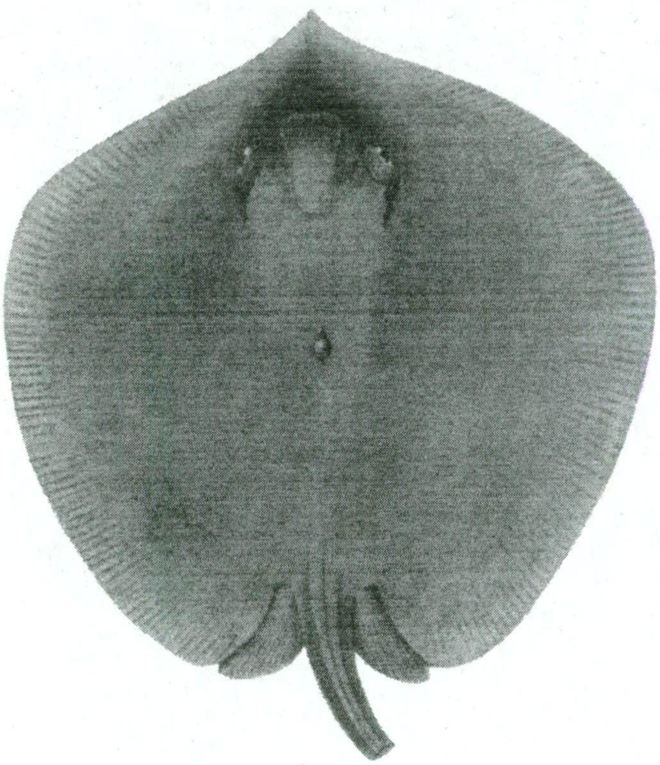


Figure 5.3.6. Representative specimen of adult *Himantura pastinacoides* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, oronasal. CSIRO H5479.03 (417 mm DW; female; Sandakan, Sabah, Malaysia). Bars 10 cm.

a)

b)

c)

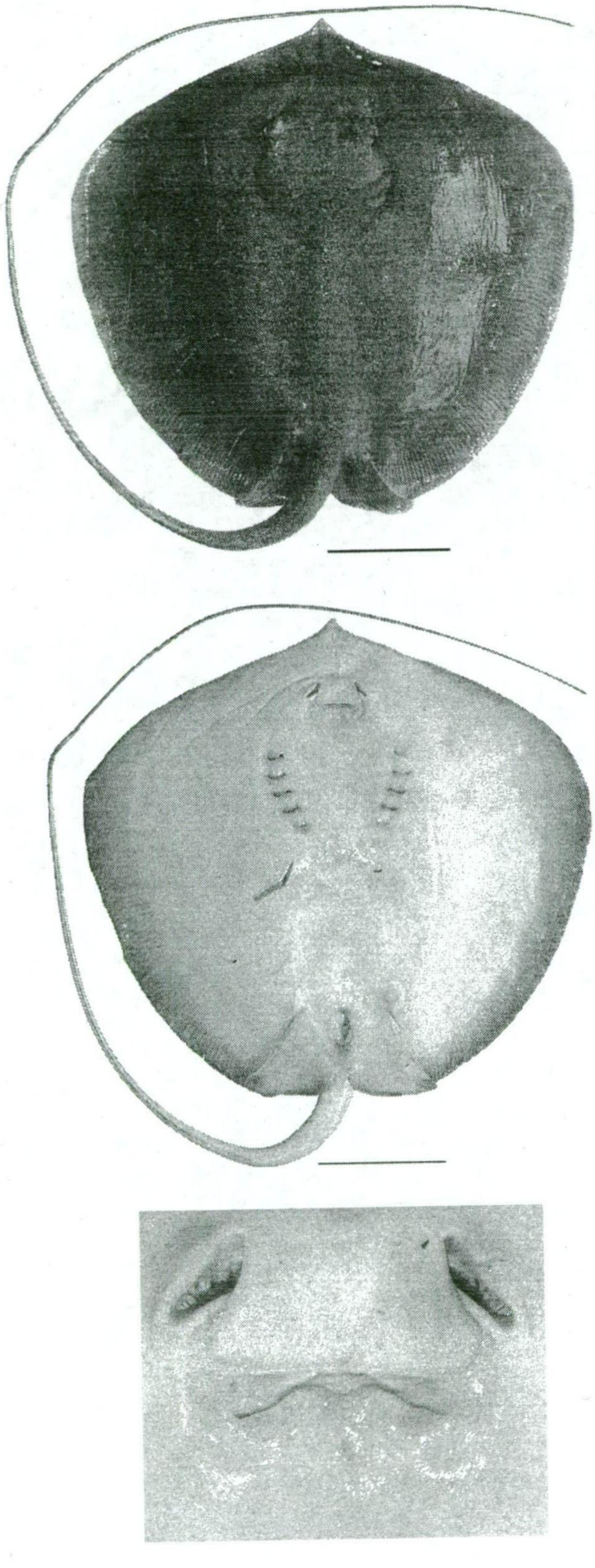
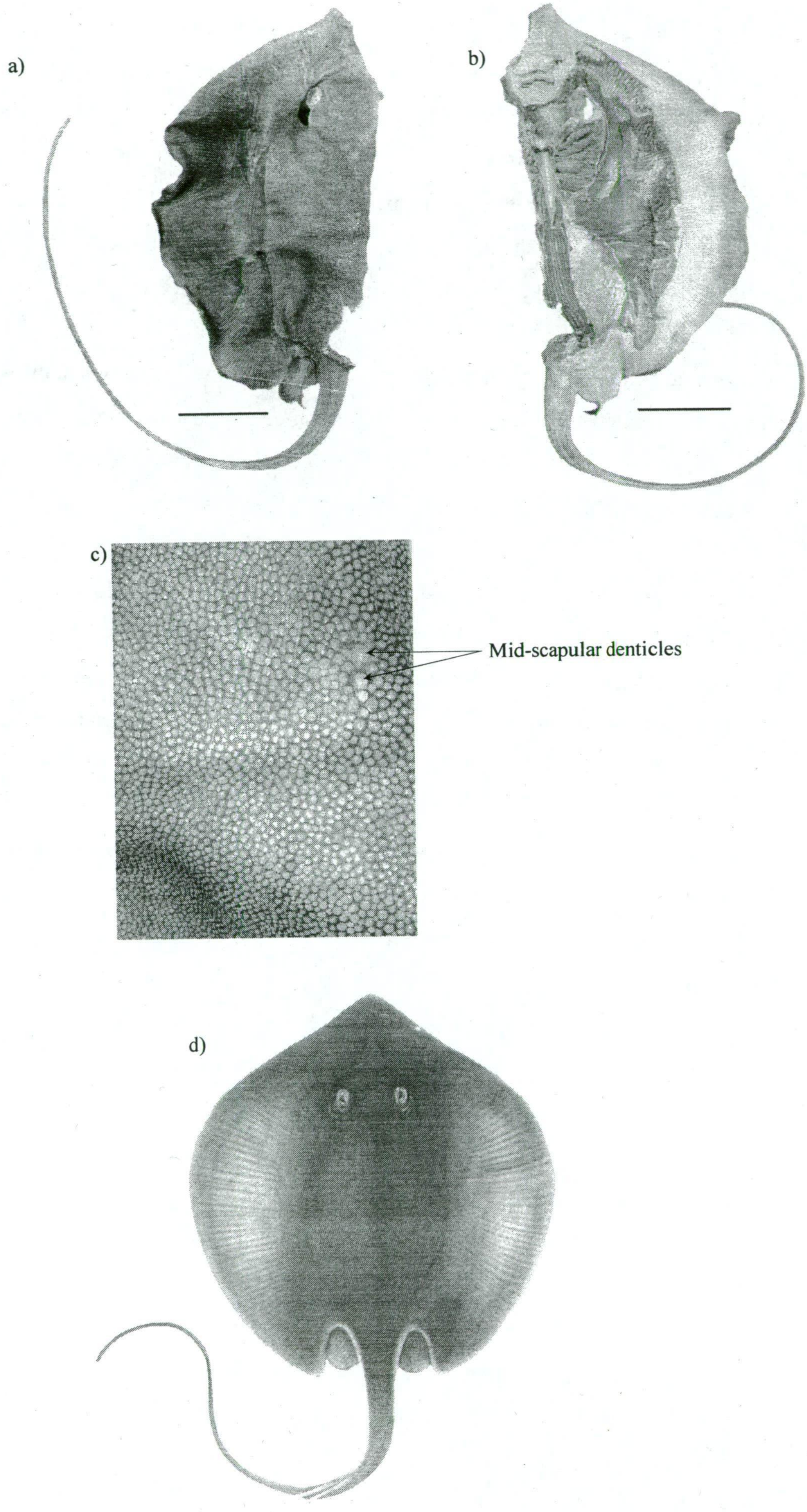


Figure 5.3.7. Holotype of *Trygon pareh* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of scapular denticles (BMNH 1867.11.28.155; 436 mm DW; female; 'East Indies'; photos and measurements by P. Last); d, illustration (reproduced from Bleeker 1877: fig. 2, pl. 557, Plagiostom. Pl. 35). Bars 10 cm.


a)
b)
c)
Mid-scapular denticles
d)

Mouth arched; lower jaw double convex; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2-4 oral papillae; medial pair simple, rounded distally, longitudinally flattened, sub-equal in size and larger than outer pair, closer to each other than outer two; outer pair located at each corner of mouth, widely separated from inner pair; outer pair small, or absent. Palate with a central longitudinal ridge of skin and two angularly positioned longitudinal ridge of skin.

Teeth small, in pavement, similar in upper and lower jaws; closely-set, crowns well separated from one another; size varying continuously lateral to symphysis, largest at or adjacent symphysis, smallest near mouth corner; cone-shaped with blunt peak. Tooth rows 23 in upper jaw, 27 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.47 (1.19-1.78) times length of fifth, 0.33 (0.35-0.54) of mouth width; distance between first gill slits 2.70 (2.31-2.97) times internasal distance, 0.45 (0.42-0.47) of ventral head length; distance between fifth gill slits 1.79 (1.42-1.91) times internasal distance, 0.30 (0.26-0.30) in ventral head length.

Squamation. — Stages of squamation with narrow overlapping size ranges. Rate of squamation relatively fast, secondary denticle band quite well developed by 230 mm DW, more or less well developed by 300 mm DW; with a prominent ovoid suprascapular denticle.

Holotype is in Stage 0 (Fig. 5.3.4): dorsal surface smooth, except for a prominent ovate suprascapular denticle (length 4.4 mm).

Stage 0: from birth (ca. 155 mm DW) — Disc entirely smooth; with a prominent ovate suprascapular denticle (length 2.8-4.5 mm).

Stages 1-2: (ca. 165 mm DW) — Development of primary, median denticle band above first synarcual almost simultaneous with the initial development of discontinuous secondary denticle patches, interorbital and on scapular region. In late part of the stage, primary band becoming inconspicuous.

Stage 4: (>220 mm DW) — Secondary patches coalesced, narrowly connected at nape, to form a continuous longitudinal band with well-defined margins. Secondary band rapidly developing by about 300 mm DW, extending forward of orbits, covering entire interorbital space, and evenly wide along midtrunk.

In late part of the stage, secondary median denticle band well developed as a continuous, broad subrectangular longitudinal band, with well-defined margins; band width exceeding interspiracular distance, broadly expanded anteriorly beside eyes; anterior margin rounded, extending well forward of orbits; naked snout ratio around 51%; posteriorly, band margin anterior of pectoral-fin insertion almost horizontal for a distance equivalent to a spiracle length, before tapering to the tail across entire dorsal surface. Denticles in band closely-set, of medium size, progressively decreasing in size towards the margin; flat heart-shaped.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine present.

Meristics. — Total pectoral-fin radials (holotype not radiographed) 129-136 (n=9); propterygium 50-53, mesopterygium 18-22, metapterygium 57-65; pelvic-fin radials 24-30 (n=5); vertebral segments 108-112 (n=8), monospondylous 43-56 (n=9), prespine diplospondylous 63-69 (n=8), and postspine diplospondylous 0 (n=9).

Colour. — Dorsal surface of holotype almost uniform light brownish; ventral surface paler (whitish), with weak evidence of relatively narrow brownish margins, but not on pelvics; tail cut at sting base.

In fresh, disc uniform dark brown to brownish green; ventral surface uniform pale in young; with narrow light brown margins in larger specimens and adults, ventral pelvic fins plain pale, light brown blotch on free posterior tip; tail dark brown, darker on dorsal half, whitish on ventral half from tail base to sting base.

Skeletal morphology. — Neurocranium of a mature male (Figs. 3.2.7j, 3.2.8j; disc width not available) with short nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval; fontanelle triangular-shaped, extending behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes elongate, posteriorly bluntly pointed; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commissure relatively narrow.

Scapulocoracoid (Fig. 3.2.10g) relatively broad, moderately high, posterior part strongly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5-3 times as high as long; mesocondyle long and narrow, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11j) broadly arched, relatively thick, median prepelvic process absent, small anterolateral processes, long dorsal iliac processes, and broadly rounded mesial ischial processes.

Mixopterygium (Fig. 3.2.12f) relatively simple; 2 basal segments; beta cartilage present as a separate element, merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, paddle-shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, oval subrectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, posterior end notched, narrowly extending to lateral surfaces.

Size. — Birth size around 150-160 mm DW; length at first maturity (males) between 430 and 460 mm DW. A 427 mm DW male specimen (CSIRO H4426.01) was determined as being an adolescent (late maturity stage 3), while a male specimen (UMS MMSK40) 479 mm DW, as mature (maturity stage 4). Females reaching to about 1000 mm DW, as based on specimens (not saved; colour print only) observed in Sandakan fish market (Sabah, Malaysia).

Etymology. — Not specified, but Bleeker implied the species was named after *Trygon pastinaca* (which he erroneously attributed Bonaparte as the author; see also remarks section), on account of its similarity to the latter.

Common name. — Round whipray.

Distribution. — This species is widely distributed throughout the inshore coastal waters off Sabah and Sarawak (Malaysia), and in waters around the Indonesian archipelago (Pengaron, Batavia) (Bleeker 1852, 1853). Reports elsewhere in the region, e.g. Sri Lankan waters (Morón *et al.* 1999) require verification.

Comparisons. — This species is very similar to *H. uarnacoides* (Bleeker), and to three new species described in the present study, i.e. *Himantura* spp. B-D. *Himantura pastinacoides* is distinguished from these species by a combination of characters, i.e. preorbital snout length about 25% DW; rectangular-shaped denticle band with well defined margins, width exceeding interspiracular distance, anteriorly broadly rounded just in front of orbits; young with large midscapular denticle, becoming inconspicuous in adults; disc uniform dark brown to brownish green; tail uniform dark brown, not banded.

Remarks. — *Trygon pastinacoides* was described based on a young, possibly neonatal, female specimen, BMNH 1867.11.28.161. Its skin is almost void of denticles, except for a single midscapular denticle, and the tail has been cut-off at the base of the sting. Ironically, Bleeker (1852) did not appear to notice the specimen being at a young life-stage, when he compared it to *T. pastinaca* and *T. akajei*. He noted the three as most closely related among the other species he described, primarily based on the shape of the disc and almost total absence of denticles on the dorsal surface of the disc. Subsequently, such comparison is in vain because the holotype specimen was a young representative. The latter two species have also now been re-assigned under the genus *Dasyatis* (see e.g. Nishida & Nakaya 1990; Cowley & Compagno 1993).

Its senior synonym, *T. pareh* Bleeker (1852), was described from an adult female specimen, BMNH 1867.11.28.155, whose denticle band is well developed. This specimen, previously dried, and presently preserved in ethanol, is badly mutilated, retaining only the skin of just over half of the left side of the disc, and with the tail intact. The denticles and denticle band on the remaining skin, nevertheless appear well-preserved and intact, as originally described. The mutilated condition of the type specimen however, was neither mentioned by Bleeker nor by others whom have examined it (e.g. Günther 1870).

The illustrated species of *T. pareh* (Bleeker 1877) however, holds a clue to this (condition of the type specimen). To the trained eye, the illustration indicates a rather disproportionate stingray, particularly the disc and denticle band shapes, and the interorbital space (P. Last pers. comm.). An imaginary reconstruction of the complete stingray based on the incomplete specimen indeed helps explain this disproportionate image (illustration and images of holotype reproduced in Figure 5.3.7). Apparently, it appears the illustrator failed to notice that the holotype was not perfectly halved (Figs. 5.3.7a, b), thus the 'too triangular' snout and 'too broadly rounded' pectoral-fin apices, and 'too narrow' space between the orbits; additionally, the pectoral-fin insertions appear 'too broadly gapped', all of which did not appear natural.

The decision that *T. pastinacoides* and *T. pareh* are synonymous was made possible by the collection of almost every possible gradient size of the species, particularly indicating development of squamation, which confirms that the former is really the young or juvenile of the latter.

However, with regards to nomenclature, although *T. pareh* was listed and described ahead of *T. pastinacoides* in the same paper by Bleeker (1852), the latter name is treated as the valid name, while the former its senior synonym. This decision is based on a provision of the 'Principle of Priority Article 23.9.1, Recommendation 23A' of the ICZN (1999), regarding reversal of precedence and desired suppression.

On the frequency of their usage, both names have not been used as available names until only very recently. The reason is perhaps because, in earlier revisions, *T. pareh* and *T. pastinacoides* have both been incorrectly listed, either together or separately, in the synonymy of other species. For example, Garman (1913) and Fowler (1941) regarded both species as a junior synonym of *H. uarnak* Forsskål, while Compagno and Roberts (1982) regarded *T. pareh* as a senior synonym of *H. alcocki* Annandale, and *T. pastinacoides* as a junior synonym of *H. uarnak* Forsskål.

Himantura pareh appeared as an available name for the first time in 1998 (Morón *et al.* 1998) since Bleeker (1852). Two varieties, apparently based on disc and tail colouration, were given in the recent paper. However, the precise description of the large specimens, particularly of the tail, suggest the species might be a misidentification of *H. gerrardi*, or either one of the new species described in the present study, i.e. *Himantura* spp. B-D.

On the other hand, *H. pastinacoides* have been listed as an available name in at least two separate papers, i.e. in Fowler *et al.* (1999), and Compagno *in* Randall and Lim (2000). Fowler *et al.* specifically stated the species as one of the 'resurrected names', based on concurrent studies by Last, Compagno and Manjaji (p. 264).

The recommendation of Article 23.9.3 thus applies to this situation, because the two conditions set by Article 23.9.1 which states 'the senior synonym has not been in use as a valid name after 1899' (Article 23.9.1.1), and 'the junior synonym has been in use for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years' (Article 23.0.1.2), are not strictly met. Furthermore, it is considered the use of the older name may threaten universality and cause confusion rather than stability, and so to maintain the use of the younger synonym, this case should be referred to the Commission for ruling under the plenary power (Article 81).

Finally, according to Article 23.9.2, the younger name (once it is approved as valid), may be qualified by the term *nomen protectum* and the invalid, but older, name (also, once the case is approved by the Commission) by the term *nomen oblitum*.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

BMNH 1867.11.28.155[c](holotype of *Trygon pareh*), BMNH 1867.11.28.161[c](holotype) ('Far East Indies'); CAS 213285 (Thailand); CSIRO H4424.01, CSIRO H4424.02, CSIRO H4424.03, CSIRO H5613.01[b,c] (Kuching, Sarawak, Malaysia); CSIRO H4426.01 (Java, Indonesia); CSIRO H5471.01[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H4921.04 [b], CSIRO H5479.02[b,c], CSIRO H5479.03, CSIRO H5479.12, CSIRO H5479.13, CSIRO H5479.14, CSIRO H5479.15, CSIRO H5480.02, CSIRO H5614.01[b,c], CSIRO H5615.01, CSIRO H5615.02, UMS MMSK7, UMS MMSK39, UMS MMSK40 (Sandakan, Sabah, Malaysia); NMV A914 (possible syntype) (Indonesia); RMNH 2461[c], RMNH 2463[c], RMNH 2464[c], RMNH 2470[c], RMNH 7437[c], RMNH 8007[c] (unspecified locality).

Himantura uarnacoides (Bleeker 1852)

Brown whipray

Figures 3.2.5o, 3.2.6n, 3.2.7s, 3.2.8r, 3.2.10p, 3.2.11o, 5.3.8-5.3.10;

Tables 5.3.7-5.3.8

Trygon uarnacoides Bleeker 1852: 72 (original description based on 5 specimens, 4 females, 180-255 mm disc width, see also Notes under description of *T. polylepis* Bleeker [1852], not figured). Two possible syntypes: BMNH 1867.11.28.210, 254 mm disc width, female; RMNH 2467, 236 mm disc width, female (measurements by P. Last). Type localities: Batavia (=Java) and Samarang (=Semarang), both in Indonesia.

Synonymy. —

Trygon bleekeri Blyth 1860: 41 (original description based on unspecified number of specimens, not figured). Possible syntype: BMNH 1892.6.17.15, 194 mm disc width (measurement by P. Last), female. Type locality: Bay of Bengal, India.

Trygon (Himantura) bleekeri: Günther 1870, 475 (listed). Locality: Bengal.

Leiobatis (Himantura) uarnakoides: Bleeker 1877, fig. a and b, pl. 561, Plagiostom. Pl. 39 (illustration of young male syntype).

Dasybatus (Himanturus) bleekeri: Garman 1913, 379 (description after Blyth).

Himantura uarnacoides: Fowler *et al.* 1999, 262 (listed). Locality: coastal Sabah, Malaysia.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape subcircular, robust, centre raised at mid-scapular, preorbital snout moderately long, weakly convex, with a distinct apical lobe, anterior disc margin strongly convex, lateral apices broadly rounded. Dorsal surface of disc uniform dark brown to blackish in young, orange-brownish in adults; ventral surface almost entirely greyish brown, narrow medial area often pale (whitish); tail dark brown, darker on dorsal half, whitish on ventral half from tail base to sting base, becoming paler towards tail tip. Secondary denticle band well developed by 300 mm DW; with two prominent wide heart-shaped suprascapular denticles.

Description. — Disc subcircular, axis of greatest width almost equal to distance from tip of snout to pectoral-fin insertion, width 0.95-1.01 times length; robust, center raised at mid-scapular, maximum disc thickness 0.09-0.14 in disc width (DW); preorbital snout moderately long, weakly concave, with a distinct apical lobe, angle 100-112^{o}; anterior margins of disc strongly concave, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.3.7-5.3.8). Pelvic fins moderately long, 17.2-19.9% DW; width across base 9.8-14.4% DW. Claspers of adult male (Fig. 3.2.5o) long, rather pointed at tip, dorsal and ventral surfaces slightly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle short, about 1/3rd of clasper length on its outer margin, weak notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 3.10-4.10 times disc width; base depressed, subcircular in cross-section, width 1.30-1.80 times height at base.

Snout moderately long, depressed; preoral snout length 3.40-4.39 times mouth width, 2.67-3.25 times internarial distance, 27.0-32.0% DW; direct preorbital snout length 1.65-2.31 times interorbital length, horizontal length 1.57-2.24 times interorbital length; snout to maximum disc width 40.9-49.7% DW; interorbital space flat; eye moderately large, diameter 37-62% spiracle length; orbits protruded, diameter 0.61-0.88 in spiracle length, interorbital distance 2.11-3.63 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, slit-like, outer margin with a weak double concavity, length 0.38-0.56 in internasal distance; internasal distance 0.37-0.47 of prenasal length, 1.79-2.44 times nostril length. Nasal curtain subrectangular, relatively broad, width 1.61-2.07 times length; lateral margin almost straight, weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, weakly concave to weakly double concave.

Mouth moderately arched; oronasal groove prominent; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2-4 well-developed papillae, rounded distally, longitudinally flattened, sub-equal in size, located near to each other.

Teeth small, similar in upper and lower jaws; closely-set, crowns well separated from one another; size varying continuously lateral to symphysis, largest at or adjacent symphysis, smallest near mouth corner. Tooth rows counts not available.

Gill opening margins smooth, straight; length of first gill slit 1.00-1.74 times length of fifth, 0.29-0.43 of mouth width; distance between first gill slits 1.96-2.28 times internasal distance, 0.36-0.43 of ventral head length; distance between fifth gill slits 1.24-1.48 times internasal distance, 0.24-0.28 in ventral head length.

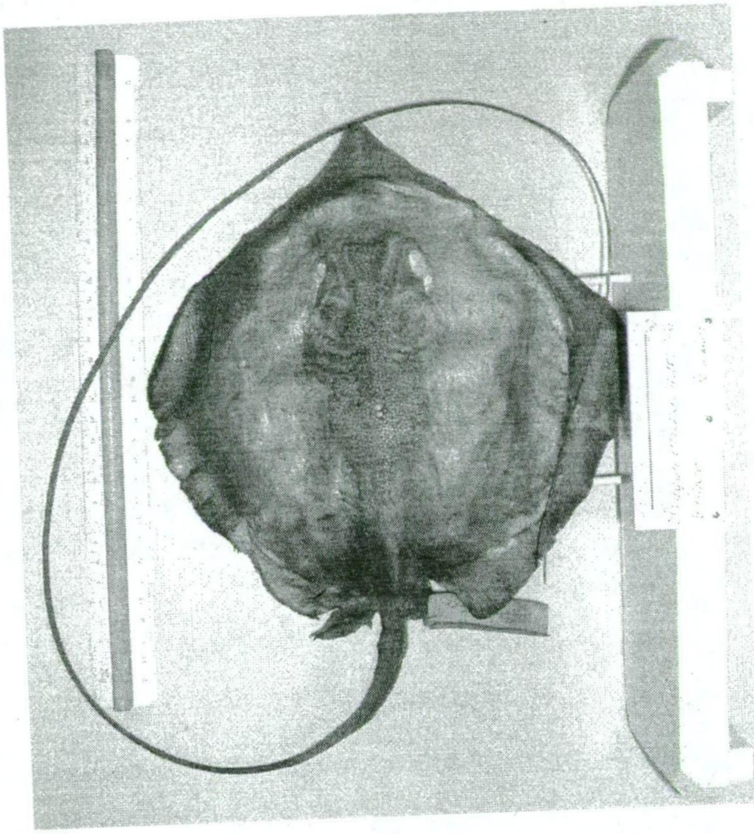
Squamation. — Stages of squamation with narrow overlapping size ranges. Rate of squamation relatively fast, secondary denticle band quite well developed by 230 mm DW, well developed by 300 mm DW; with two prominent wide heart-shaped suprascapular denticles.

Stages 0-1: from birth (ca. 180-200 mm DW) — Disc of newborns with a sub-primary denticle band, and single wide heart-shaped embryonic suprascapular denticle (length 3.4 mm) still enveloped under a thin layer of skin; other surfaces smooth.

Stage 2: (ca. 225 mm DW) (Figs. 5.3.10) — Denticles simultaneously appearing interorbital and scapular around suprascapular denticle, forming two separate patches weakly connected by the primary band; primary denticle band remain inconspicuous; second smaller wide heart-shaped suprascapular denticle appearing. Denticles on interorbital minute conical, widely and evenly distributed above fontanelle; those on scapular flat narrow heart-shaped, confined to adjacent suprascapular denticles; tail void of denticles.

Figure 5.3.8. One of five possible female syntypes of *Himantura uarnacoides* in dorsal view (a), and close-up of scapular denticles (b). RMNH 2467 (236 mm DW; Batavia). Photos and measurements by P. Last.

a)



b)

Figure 5.3.9. Illustration of *Himantura uarnacoides* (reproduced from Bleeker 1877: fig. a, pl. 561, Plagiostom. Pl. 39).

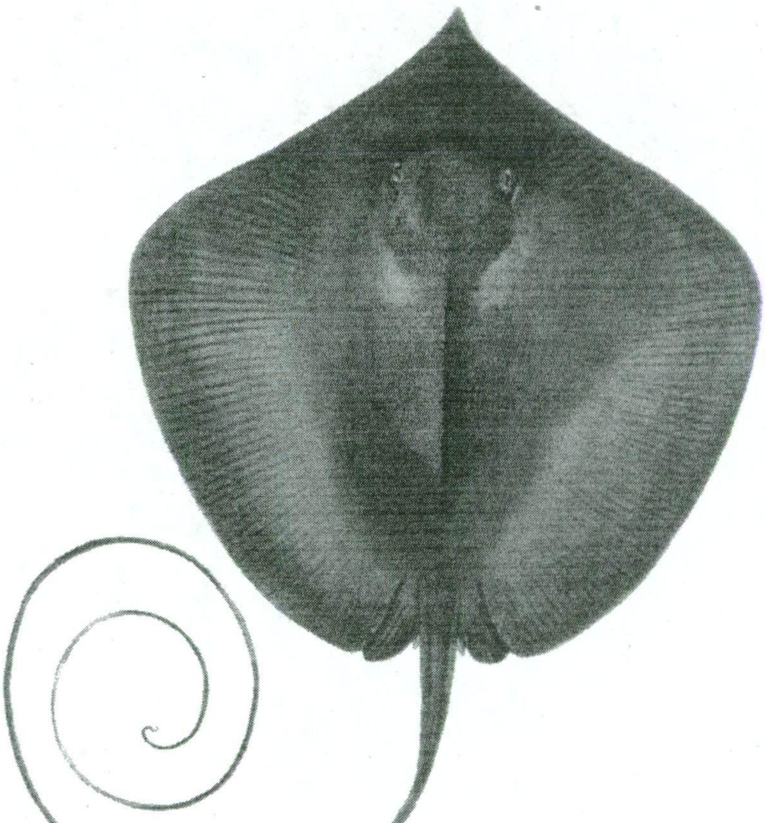
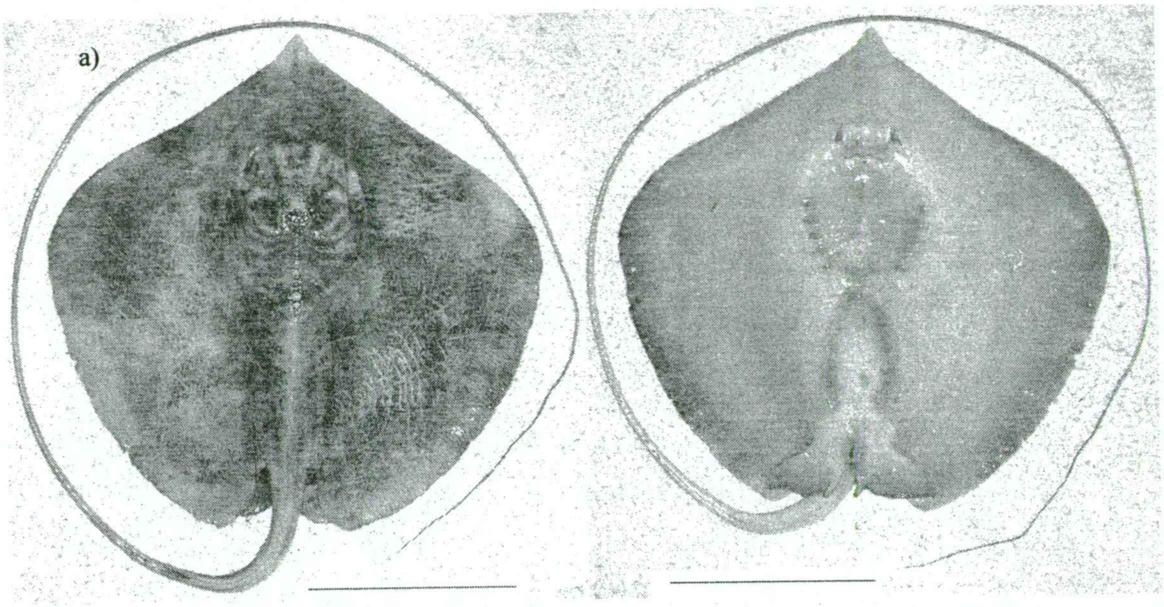
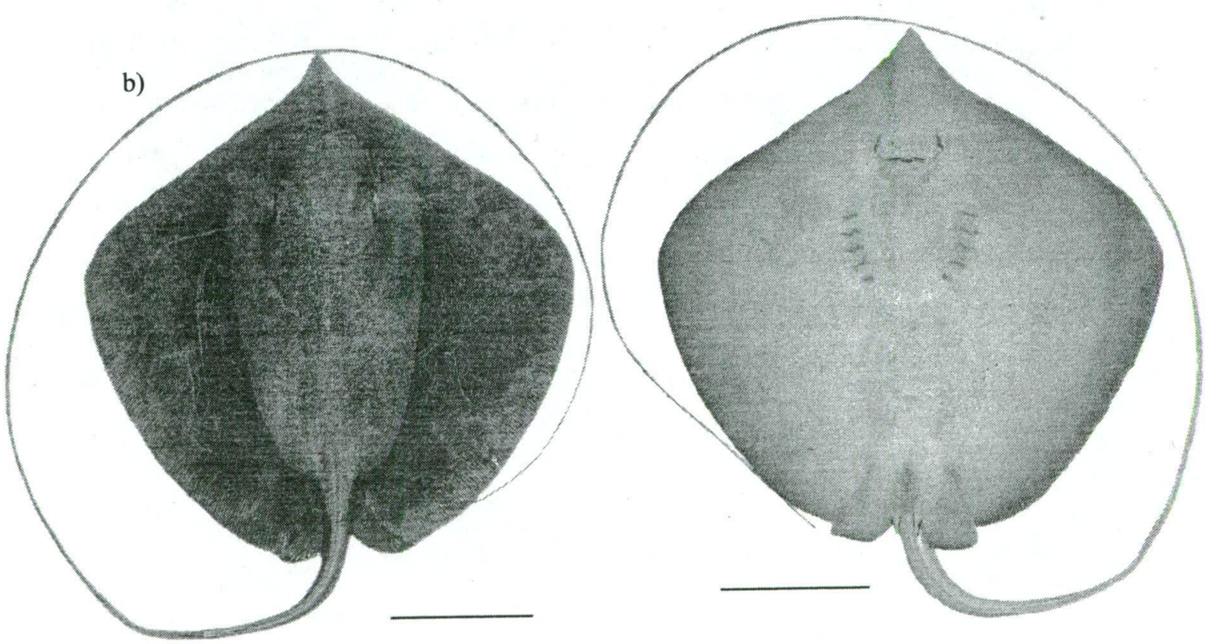


Figure 5.3.10. Representative specimens of *Himantura uarnacoides* indicating squamation. a, 243 mm DW (CSIRO H5616.04; immature male; Sandakan, Sabah, Malaysia); b, 788 mm DW (SMKK SKN24-4496; immature male; Sandakan, Sabah, Malaysia; photos by G. Yearsley). Bars 10 cm.

a)



b)



As the development progresses, more denticles appearing interorbital and above scapular region; denticles in median connective band adjacent primary band much less developed, resulting in a shield-like band shape above scapular (i.e. anteriorly truncated, posteriorly narrowing to a point above the abdomen); band margin irregular, moderately well-defined; denticles appearing on dorsal surface behind sting. Denticles uniform flat narrow heart-shape, closely spaced; size subequal, only slightly smaller on head and margins.

Stage 4: (ca.240 mm DW) — Secondary denticle band well developed as a continuous subrectangular longitudinal band, with well-defined margins; anteriorly constricted at nape, reaching to just in front of orbits; band slightly convex at scapular, posteriorly extending irregularly above abdomen, terminating at level just in front of pectoral-fin insertion; two prominent suprascapular denticles. One of the possible syntypes (i.e. RMNH 2467, 236 mm DW) examined (P. Last pers. comm.) is in early part of Stage 4 (Fig. 5.3.8).

During late part of the stage (>330 mm DW), secondary median denticle band a regular, continuous subrectangular longitudinal band with well-defined margins; band width exceeding interspiracular distance, broadly expanded anteriorly beside eyes; anteriorly extended well forward of orbits, margin broadly rounded, slightly constricted anterolateral of orbits; naked snout ratio 62%; posteriorly narrowing evenly, truncated just anterior to pectoral-fin insertion before continuing narrowly onto tail across entire dorsal surface. Denticles in band closely-set, of medium size, progressively decreasing in size towards the margin; flat heart-shaped.

Stages 3, 5 and 6 not applicable for this species.

Single elongate stinging spine present.

Meristics. — Total pectoral-fin radials 141-147 (n=8); propterygium 52-59, mesopterygium 23-30, metapterygium 58-64; pelvic-fin radials 23-29 (n=7); vertebral segments 104-111 (n=8), monospondylous 46-55, prespine diplospondylous 51-62, and postspine diplospondylous 0.

Colour. — In fresh, dorsal surface of disc including tail, uniform dark brown to blackish in young, orange-brownish in adults; ventral disc surface almost entirely greyish brown, narrow medial area often pale (whitish). Fresh and preserved specimens often found with scratch markings or pale abraded areas above, as the dorsal colouration is easily removed. Tail uniform dark brown, darker on dorsal half, whitish on ventral half from tail base to sting base, becoming paler towards tail tip.

Skeletal morphology. — Neurocranium of 810 mm DW mature male (Figs. 3.2.7s, 3.2.8r) with short nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval; fontanelle triangular-shaped, extending behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes elongate, posteriorly pointed; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commissure relatively broad.

Scapulocoracoid (Fig. 3.2.10p) relatively broad, moderately high, posterior part strongly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; two small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11o) broadly arched, relatively thick, median prepelvic process absent, small anterolateral processes, moderately long dorsal iliac processes, and narrowly rounded mesial ischial processes.

Mixopterygium of adult males unknown.

Size. — Birth size around 180 mm DW; length at first maturity (males) between 500 and 600 mm DW. A 427 mm DW male specimen (CSIRO H5479.19) was determined as being an adolescent (maturity stage 3), while a male specimen (CSIRO H5470.01) 810 mm DW, as mature (maturity stage 4). As for females, the largest specimen observed, was gravid at 965 mm DW (CSIRO H5481.02, only partly saved; its newborn saved as CSIRO H5481.03).

Etymology. — According to Bleeker, the species was named after *Trygon uarnak* (which he erroneously attributed Müller & Henle as the authors), on account of its similarity to this species.

Common name. — Brown whipray; White-nosed whipray (Fowler *et al.* 1999); Bleekers whipray (Last & Compagno 1999).

Distribution. — Widely distributed throughout inshore coastal waters off Sabah and Sarawak (Malaysia), Thailand and Indonesia. One specimen was caught in an ox-bow lake (saltwater) near the mouth of Kinabatangan River (Sabah).

Comparisons. — Specimens particularly large size and adults, may be confused with *H. pastinacoides* (Bleeker), *H.* sp. E and *H.* sp. F (the latter two described in this study). *Himantura uarnacoides* is distinguished from these species by a combination of characters, i.e. preorbital snout length about >25% DW; orbits >60% spiracle length; presence of oral papillae; rectangular-shaped denticle band with well defined margins, width greatly exceeding interspiracular distance, anteriorly extended onto snout, narrowly rounded in front of orbits; two large midscapular denticles, remaining conspicuous in adults; disc uniform dark brown to blackish in young, orange-brownish in adults; tail uniform dark brown, not banded.

Remarks. — *Trygon uarnacoides* was described based on five specimens, ranging between 180-255 mm DW, all of which Bleeker (1852) noted as being young. However, unlike in his description of the other *Trygon*'s, Bleeker did not particularly mention the habitat of this species as marine or 'from the sea' (translation by P. Aukland), suggesting either the specimens were indeed not all are entirely from the marine environment, or that such information may have been unintentionally excluded, but which is less likely. This is supported by the fact that confirmed reports of the species are based on specimens obtained from locations adjacent mangrove shores (i.e. brackishwater) (e.g. Fowler *et al.* 1999; pers. observation), and further, the discovery of a young specimen of this species (SMKK KTG 1 12698, 262 mm DW) from an ox-bow lake near the mouth of the Kinabatangan River (Sabah, Malaysia) (S. Mycock and R. Cavanagh pers. comm. 1998).

Bleeker compared this new species with *H. uarnak*, which he considered as most similar to it, hence the name. However, he also noted several differences between the two species of similar size, namely that the former lacks the dorsal disc spotting, eyes smaller and squamation less developed. Two of the putative syntypes (BMNH 1867.11.28.210, 254 mm DW; RMNH 2467, 236 mm DW, Fig. 5.3.8) examined were observed as having similar squamation stage as that of the illustrated male (Fig. 5.3.9; Bleeker 1877), i.e. secondary denticle band in mid-Stage 4.

It the present study, it was found that not only are there differences in the squamation rate between *H. uarnacoides* and *H. uarnak*, but even their size at birth vary. The birth size of *H. uarnacoides* is around 180 mm DW, whilst bigger at around 260 mm DW for *H. uarnak*. The squamation rate of *H. uarnak* although relatively fast, is slower compared to *H. uarnacoides*, having its secondary denticle band quite well developed by about 300 mm DW (see squamation section under species description heading for *H. uarnak*).

Trygon bleekeri Blyth, a species described from the Bay of Bengal, is herein considered as a junior synonym of *H. uarnacoides*. A possible syntype (BMNH 1892.6.17.15, 194 mm DW) of the species exists in the British Museum of Natural History, although Blyth himself did not specify any types or even the number of specimen used in describing the species. The specimen, examined and photographed by P. Last (pers. comm.) is a young female, its tail intact, and dorsal surface of the disc with only a subprimary denticle band and a prominent pearl-shaped midscapular denticle.

As with *H. pastinacoides*, the decision that *T. bleekeri* is synonymous with *H. uarnacoides* was made possible by the collection of almost every possible gradient size of the species, particularly indicating development of squamation, confirming the two as conspecifics. Moreover, Blyth's description of the species concerning disc colouration, disc shape, and midscapular denticle, i.e. '... plain dark brown above and below with a narrowish white median patch on belly. Peak, or anterior junction of the pectorals (snout), considerably more prolonged and pointed than in the others. ... The usual large round tubercle on centre of back, and commonly three smaller, set in form of a triangle, before it and three similar behind it.', further support this decision.

On the frequency of their usage, both *bleekeri* and *uarnacoides* have appeared in less than 25 works, the former having been listed as an available name in more publications compared with the latter. Specifically, *bleekeri* has appeared in more than 10 works by at least 10 authors (e.g. Günther 1870; Day 1878, 1889; Annandale 1909; Garman 1913; Anon 1955; Compagno & Roberts 1982; Talwar & Kacker 1984; Bianchi 1985; Nishida 1990; De Bruin *et al.* 1995; Compagno 1999a, c; Ross & Schäfer 2000; Eschmeyer On-Line, ver. February 15, 2002), not including Blyth's own work (1860).

On the other hand, the *uarnacoides* appeared in fewer numbers of works (i.e. Fowler *et al.*; Last & Compagno 1999; and Compagno *in* Randall and Lim 2000), even when Bleeker's own work (1852) is included. Two authors (i.e. Compagno and Last) are involved in most of these works. Fowler *et al.* specifically stated *H. uarnacoides* as one of the 'resurrected names' (the other being *H. pastinacoides*), based on concurrent studies by Last, Compagno and Manjaji (p.264). Whereas, according to P. Last (pers. comm.) *H. bleekeri* was erroneously listed in Last and Compagno, hence no species account given for this species but instead a species account for *H. uarnacoides* was provided, although it was not mentioned in the list (p.1408).

Thus, with reference to the rulings under ‘Article 23.9 on the Reversal of precedence’ of the ICZN (1999), although the name *bleekeri* has been in use more frequently compared to *uarnacoides*, it is noted that its usage in the numerous publications cited earlier are merely listings in abstracting publications. Such work, according to Article 23.9.6, ‘must not be taken into account in determining usage under Articles 23.9.1.1 and 23.9.1.2’.

These latter two conditions set by Article 23.9.1 which states ‘the senior synonym has not been in use as a valid name after 1899’ (Article 23.9.1.1), and ‘the junior synonym has been in use for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years’ (Article 23.0.1.2), are thus irrelevant in this particular case. Hence, based on the ‘Article 23 Principle of Priority’ of the ICZN, the available name applicable to this taxon is *H. uarnacoides*, which is also the older name.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CAS 213287(1of2), CAS 213287(2of2), CAS 213289 (Thailand); H4426.25, H4426.26, CSIRO H4426.31[b] (Java, Indonesia); CSIRO H4213.03[b], CSIRO H4919.06[b], CSIRO H4919.07[b], CSIRO H4919.08[b], H4921.01, H4921.02, H4921.03, CSIRO H5479.01[b], CSIRO H5479.16, CSIRO H5479.17, CSIRO H5479.18, CSIRO H5479.19, CSIRO H5481.02, CSIRO H5481.03, CSIRO H5616.01, CSIRO H5616.02, CSIRO H5616.03, CSIRO H5616.04, CSIRO H5616.05, CSIRO H5616.06, SMKK SKN24-4496, UMS MMSK45, UMS MMSK46, UMS MMSK53 (Sandakan, Sabah, Malaysia); CSIRO H5470.01[b,e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H5472.03 (Kuching, Sarawak, Malaysia); MTUF 30000 (India); RMNH 2467[c](possible syntype), RMNH 7441 (Batavia, Indonesia); SMKK KTG112698 (Kinabatangan River, Sabah, Malaysia).

Himantura sp. E

Hortles whipray

Figures 3.2.5t, 3.2.6q, 3.2.7x, 3.2.8w, 3.2.9l, 3.2.10t, 3.2.11t, 3.2.12m, 5.3.11-5.3.12; Tables 5.3.9-5.3.10

Synonymy. —
Nil.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape subcircular, flat, center slightly raised at mid-scapular, preorbital snout extremely long, broadly concave, with a distinct apical lobe, anterior disc margin strongly concave, lateral apices broadly rounded. Mouth floor with a thin skin fold, no oral papillae. Dorsal surface of disc dark brown; ventrally uniform pale (whitish), disc edge entirely blackish, disc margin including free posterior margin of pelvic fins with narrow dark brownish margin; margin of nostrils, nasal curtain, and gill slits dark (blackish); tail dark brown, becoming blackish behind sting; ventrally pale (whitish) along a narrow area at tail base, becoming blackish from below sting base. Secondary denticle band well developed, greatly expanded beside eyes and extending to more than half of snout anterior orbits, following anterior profile of disc.

Description. — Disc subcircular, width 0.89-0.92 in length; flat, center slightly raised at mid-scapular, maximum disc thickness 0.08-0.11 in disc width (DW); preorbital snout extremely long, broadly concave, with a distinct apical lobe, angle 96-99^{O}; anterior margins of disc strongly concave, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.3.11-5.3.12). Pelvic fins moderately long, 17.1-21.4% DW; width across base 11.0-12.0% DW. Claspers of adult male (Fig. 3.2.5t) long and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle short, about 1/3rd of clasper length on its outer margin, weak notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.90-3.13 times disc width; base depressed, subcircular in cross-section, width 1.22-1.56 times height at base.

Snout extremely elongated, depressed; preoral snout length 4.69-5.09 times mouth width, 3.33-3.77 times internarial distance, 37.1-38.7% DW; direct preorbital snout length 2.52-3.04 times interorbital length, horizontal length 2.45-2.96 times interorbital length; snout to maximum disc width 51.7-57.9% DW; interorbital space flat; eye small, diameter 22-31% spiracle length; orbits not protruded, diameter 0.40-0.53 in spiracle length, interorbital distance 3.81-6.20 times orbit. Spiracles rectangular-shaped, very large, situated dorso-laterally. Nostrils moderately large, laterally slightly expanded, outer margin weakly concave, length 0.32-0.59 in internasal distance; internasal distance 0.31-0.36 of prenasal length, 1.70-3.11 times nostril length. Nasal curtain subrectangular, relatively broad, width 1.72-1.87 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave, falling just short of mouth.

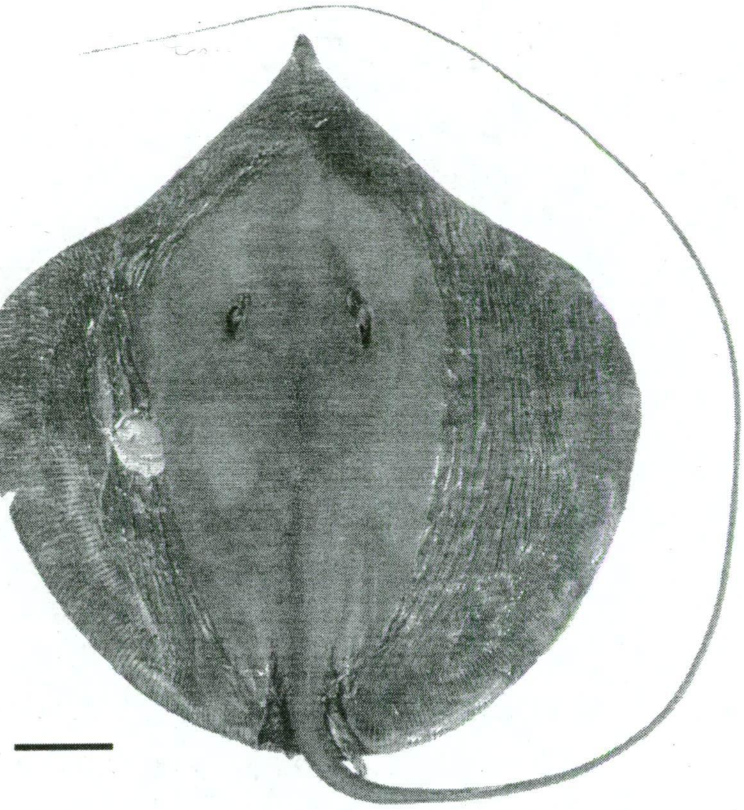
Mouth slightly arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with a thin skin fold, no oral papillae. Palate with single central longitudinal ridge of skin.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak. Tooth rows 21-25 in upper jaw, 24-28 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.32-1.84 times length of fifth, 0.32-0.44 of mouth width; distance between first gill slits 1.59-1.82 times internasal distance, 0.29-0.33 of ventral head length; distance between fifth gill slits 1.21-1.30 times internasal distance, 0.22-0.24 in ventral head length.

Squamation. — Stages of squamation with broad size ranges. Secondary denticle band well developed, greatly expanded beside eyes and extending to more than half of snout anterior orbits; its development simultaneous with center of disc appearing raised.

Figure 5.3.11. Representative specimen of *Himantura* sp. E in dorsal and ventral views. CSIRO H5155.01 (707 mm DW; mature male; Minajerwi River estuary, Irian Jaya, Indonesia; photos by T. Carter). Bars 10 cm.



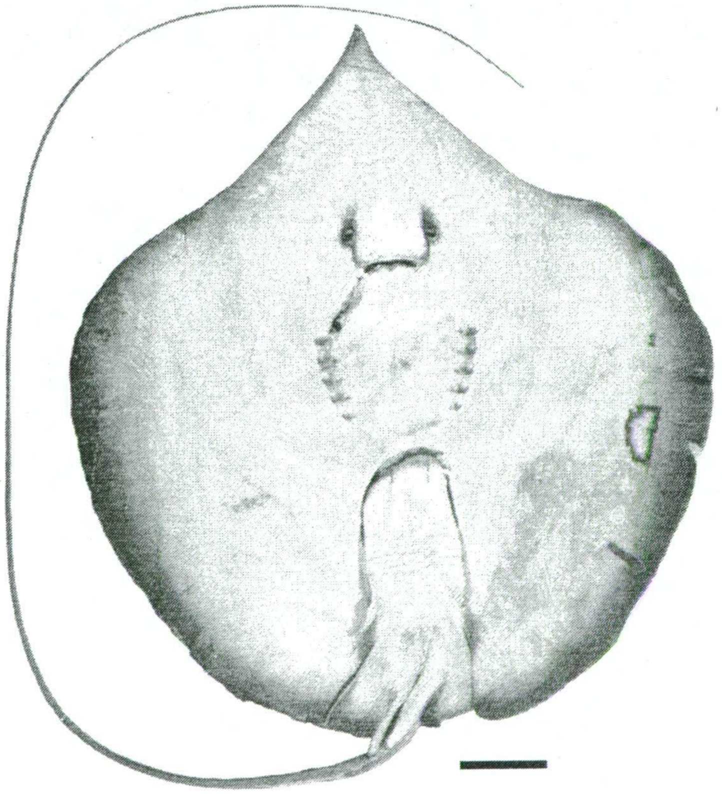
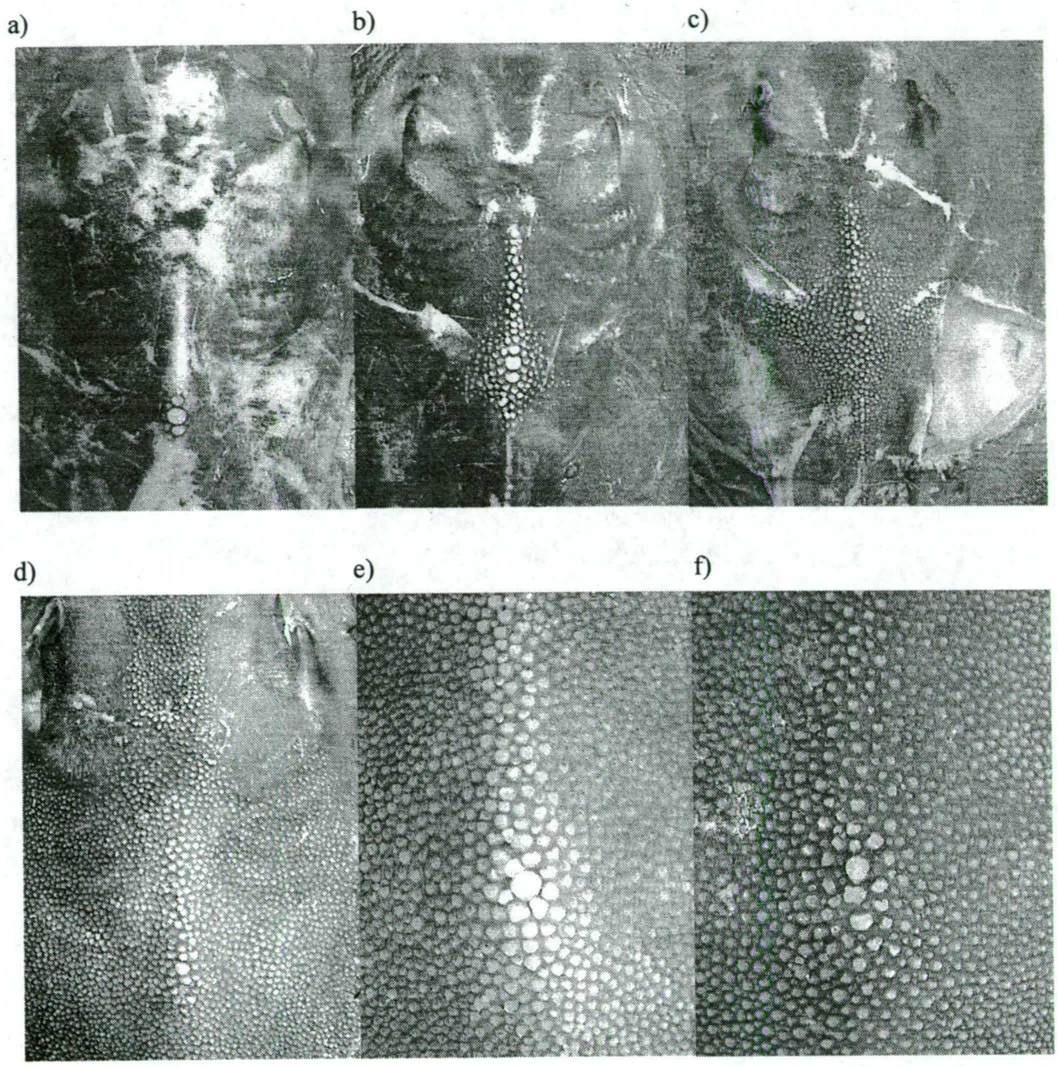


Figure 5.3.12. Representative specimens of *Himantura* sp. E from Irian Jaya indicating squamation. a, 246 mm DW (CSIRO H4917.01; female; Poriri Island); b, 268 mm DW (CSIRO H5285.01; immature male; main Ajkwa River estuary); c, 282 mm DW (CSIRO H4915.01; immature male; main Ajkwa River estuary); d, 327 mm DW (CSIRO H4916.01; female; main Ajkwa River estuary); e, 430 mm DW (CSIRO H4549.02; female; Ajkwa River estuary); f, 707 mm DW (CSIRO H5155.01; mature male; Minajerwi River estuary).


a)
b)
c)
d)
e)
f)

Stage 0: from birth (ca. ?240 mm DW) (Fig. 5.3.12a) — The question mark denotes the likely size for this stage, as there is no representative specimen available for study; the smallest specimen (CSIRO H4917.01, 246 mm DW, female) is almost void of denticles, except for three enlarged ovate suprascapular denticles, a few barely noticeable minute denticles on snout lobe, and numerous minute conical denticles on tail.

Stage 2: (ca. 250 mm DW) (Fig. 5.3.12b, c) — Development of secondary median denticle patch adjacent suprascapular denticles.

As the development progresses, band extending rapidly anteriorly as a narrow row above first synarcual, slightly expanded laterally at midscapular, and much less posteriorly. Such squamation rate continuing until late part of the stage, with more denticles appearing anterior the suprascapular denticles, and much less posteriorly, resulting in a patch with broad subtriangular in shape on area above the gills and mid-disc. Denticle patch with moderately well-defined margin; denticles flat narrow heart-shape, closely-set, almost imbricated, large and small sized denticles interspersed; size largest along the middle, gradually decreasing towards margin of the band.

Stage 4: (>300 mm DW) (Fig. 5.3.12d) — In early part of this stage (320 mm DW), scapular denticle patch extended anteriorly to interorbital as a narrow band, posteriorly gradually narrowing to a point just anterior pectoral-fin insertion, forming a scoop-shaped patch.

During late part of the stage (>400 mm DW) (Fig. 5.3.11), secondary median denticle band a regular, continuous subrectangular longitudinal band with moderately well-defined margins; band width greatly exceeding interspiracular distance, broadly expanded beside eyes; anteriorly extended well forward of orbits, margin narrowly angular, following anterior profile of disc, pointed medially; naked snout ratio 35%; posteriorly narrowing gradually evenly, truncated at pectoral-fin insertion before continuing onto tail across entire dorsal surface. A few erect denticles present on anterior snout margin. Denticles in band closely-set, of medium size, progressively decreasing in size towards the margin; flat heart-shaped interspersed with smaller irregularly shaped interstitial denticles.

Stages 3, 5 and 6 not applicable for this species.

One to two elongate stinging spines present.

Meristics. — Total pectoral-fin radials 136-144 (n=6); propterygium 55-59, mesopterygium 27-31, metapterygium 51-57; pelvic-fin radials 20-27 (n=6); vertebral segments 99-102 (n=6), monospondylous 41-47 (n=5), prespine diplospondylous 53-59 (n=5), and postspine diplospondylous 0 (n=6).

Colour. — In fresh, disc uniform dark brown; ventrally uniform pale (whitish), disc edge entirely blackish, disc margin including free posterior margin of pelvic fins with narrow dark brownish margin; margin of nostrils, nasal curtain, and gill slits dark (blackish). Tail dark brown on dorsal and lateral surfaces near its base, becoming blackish behind sting; ventrally pale (whitish) along a narrow area at tail base, becoming blackish from below sting base.

Skeletal morphology. — Neurocranium of 327 mm DW female (Figs. 3.2.7x, 3.2.8w) with short nasal capsules, anterior edge broadly angular, broadly concave medially; nasal apertures transversely oval; fontanelle triangular-shaped, extending far behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes short, beak-like, posteriorly pointed; supraorbital crests low, concave along orbital margin; sphenopterotic ridge a narrow ledge with straight margins, without any processes; lateral commisure broad.

Scapulocoracoid (Fig. 3.2.10t) relatively broad, very low, posterior part weakly extended in lateral view; lateral face subrectangular, with broad base extended upwards to broad articular condyle at tip of scapular process; a small postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle low and short, 2 times as high as long; mesocondyle long and moderately broad, separated from metacondyle by deep notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11t) narrowly arched, relatively thick, median prepelvic process prominently present, small anterolateral processes, moderately long dorsal iliac processes, and small mesial ischial processes.

Mixopterygium of 707 mm DW mature male (Fig. 3.2.12m) relatively simple; 3 basal segments; beta cartilage present as a separate element, merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, paddle -shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, narrow lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, oval subrectangular, and scoop-shaped; terminal tip of axial cartilage elongate, tip pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, and narrowly extending to inner lateral surface.

Size. — Neither birth size nor length at first maturity of males and females are known. Two male specimens 268 and 282 mm DW, are determined as immature (maturity stage 2), while a male specimen (CSIRO H5155.01; Fig. 5.3.11) 707 mm DW, as mature (maturity stage 4), based on the clasper development. A moderately large female, 430 mm DW (CSIRO H4549.02) is probably not mature.

Etymology. — Nil.

Common name. — Hortles whipray; in honour of Dr. Kent Hortle who first reported the occurrence of this large whiptailed stingray from Irian Jaya, and then collected specimens for further study.

Distribution. — Western and southern Irian Jaya.

Comparisons. — *Himantura* sp. E is closest to *H. uarnacoides* (Bleeker 1852), and *H.* sp. F (this study), all three with plain disc colour, similar in overall disc shape, and with a plate-like denticle band. However, in comparing between the three, this new species and *H.* sp. F are most similar, almost throughout their life stages, while becoming similar to large (>800 mm DW) specimens of *H. uarnacoides*. Character similarities shared by *H.* sp. E and *H.* sp. F include the absence of oral papillae (none in the former, replaced by a thin skin fold in the latter), and both with reticulate pattern of the ventral lateral line canal system (Fig. 3.2.6q).

Himantura sp. E is dark brown dorsally, whereas *H.* sp. F is pale brown to greyish dorsally. Moreover, in the former, upper border around the eye is distinctly black, spiracles margins darker, and ventral disc margin blackish (even with large mature male).

The squamation of *H.* sp. E differ from *H.* sp. F by the size of the denticles in the band (i.e. slightly larger, probably due to slower development, and small denticles interspersed among larger ones), presence of enlarged midscapular denticles (1 or 2), presence of erect denticles on upper anterior snout margin, and band margin not quite as well-defined.

Remarks. — The type locality of this species in waters around Irian Jaya/ Papua New Guinea, precludes the possibility of it being conspecific with a previously described species from Taiwan *Dasyatis microphthalma* Chen (1948). The locality is far-off, and is outside the range of the Taiwanese fishing fleet back in 1940's (see also remarks under species heading of *H.* sp. F).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CSIRO H4549.02, CSIRO H4915.01[e], CSIRO H4916.01, CSIRO H5285.01 (Ajkwa River estuary Irian Jaya, Indonesia); CSIRO H5155.01[a,e] (Minajerwi River estuary, Irian Jaya, Indonesia); CSIRO H4917.01 (Poriri Island, Irian Jaya, Indonesia).

Himantura sp. F

Tubemouth whipray

Figures 3.2.7y, 3.2.8x, 3.2.9m, 3.2.10u, 3.2.11u, 5.3.13-5.3.14;

Tables 5.3.11-5.3.12

Synonymy. —

Nil.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc anteriorly produced subcircular, flat, center slightly raised at mid-scapular, snout extremely elongate, apex acute; orbit extremely small; dorsal surface with band of plate-like denticles, thorns absent; mouth highly protrusible; pelvic girdle with prominent lateral prepelvic processes; pectoral-fin radials 144; pelvic-fin radials 26-29; no oral papillae; dorsal disc uniform pale brown to greyish, uniformly white ventrally; oronasal area and gill slits dark.

Description. — Disc rhomboidal, width 0.88-0.90 times length; axis of greatest width almost equal to distance from tip of snout to pectoral-fin insertion; suprascapular region not raised, almost flat, maximum disc thickness 0.11-0.13 in disc width (DW); preorbital snout long, pointed apical lobe relatively narrow and distinct, angle 96.5-97.5^{o}; anterior margins of disc strongly concave, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.3.13-5.3.14). Pelvic fins short, 23.3-24.0% DW; width across base 13.9-16.4% DW; capable of strong forward rotation, directed laterally in two specimens examined. Mature male specimen not available for examination of clasper structure. Tail slender and whiplike, tapering gently toward sting (tail mutilated, only tail base remaining in the only two voucher specimens); base depressed, suboval in cross-section, width 1.68-1.75 times height at base.

Snout extremely long, depressed; preoral snout length 4.34-4.38 times mouth width, 3.72-4.28 times internarial distance, 35.5-37.1% DW; direct preorbital snout length 2.64-2.66 times interorbital length, horizontal length 2.60-2.61 times interorbital length; snout to maximum disc width 52.2-56.8% DW; interorbital space flat; eye very small, diameter 17-22% spiracle length; orbit diameter 31-41% spiracle length, interorbital distance 4.19-6.28 times orbit. Spiracles tear-shaped, very large, situated dorso-laterally. Nostril small, slit-like, outer margin with a weak concavity, length 0.38-0.41 in internasal distance; internasal distance 0.28-0.33 of prenasal length, 2.46-2.62 times nostril length. Nasal rachi 64. Nasal curtain rectangular, relatively narrow, width 1.85-1.87 times length; joined to upper jaw by a narrow frenum; lateral margin almost straight to weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, weakly concave to weakly double concave.

Mouth not arched; lower jaw almost horizontal, extremely protrusible, tubular when extended (Fig. 5.3.14b), capable of extending outward a distance about equal to width of the oronasal flap; oronasal groove prominent, deep. Mouth floor with a thin skin fold, no oral papillae; palate with single central longitudinal ridge of skin.

Teeth small, closely-set in pavement, similar in upper and lower jaws; cone-shaped with blunt peak; crowns well separated from one another; size continuously increasing lateral to symphysis, largest at or adjacent symphysis, smallest near mouth corner; tooth rows 29-34 in upper jaw, 31-36 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.32-1.36 times length of fifth, 0.42 of mouth width; distance between first gill slits 2.27-2.37 times internasal distance, 0.34-0.36 of ventral head length; distance between fifth gill slits 1.64-1.82 times internasal distance, 0.26 in ventral head length.

Squamation. — Both specimens examined are in late Stage 4: (>340 mm DW) (Figs. 5.3.13-5.3.14); secondary denticle band well developed, shield-like, ovoid, more acute anteriorly, with sharply-defined margins; broadest just behind orbit level; extending well forward of orbits, subtriangular, following profile of outer disc margin, a few isolated denticles extending forward of main band towards snout tip in specimens exceeding 500 mm DW; length of naked distal area of snout 21% of horizontal preorbital snout length; strongly convex beside eyes; margin adjacent pectoral-fin insertion broadly convex, narrowly truncate at junction with narrower caudal band; extending posteriorly over almost entire upper surface of tail.

Denticles in abdominal band very small, increasing progressively in size with age; in two distinct sizes centrally, smaller interstitial denticles interspersed between larger denticles; terminating abruptly at margin of band, marginal denticles similar in size to interstitial denticles; larger interorbital and scapular denticles subequal in size; 1-4 narrow, ovate suprascapular denticles with size of (up to 17 mm in length and 3 mm in width in largest specimen), arranged randomly over nuchal region, enlarged thorns absent; interorbital denticles subequal in size in orbito-nuchal area; conical denticles mostly present along midline to tail. Ventral surface of disc and tail anterior of sting origin naked; small, sparsely distributed conical denticles on tail beyond sting origin.

Stages 3, 5 and 6 not evident in this species.

Stinging spines missing in both specimens examined.

Meristics. — Total pectoral-fin radials (144, n=2); propterygial radials (63-65), mesopterygial (20-22) and metapterygial (59). Total pelvic-fin radials (26-29). Monospondylous centra (45-46); caudal centra indeterminate, tail removed.

Colour. — Disc and tail, uniform greyish to light brown dorsally (becoming slightly darker in preservative); spiracular margins and orbital membranes white. Ventral surface of disc and tail uniformly white; viscera evident as dark patches near gills and over body cavity; anterior margin of cloaca dusky; upper distal half of pelvic fins weakly banded, palest submarginally.

Figure 5.3.13. Representative specimen of *Himantura* sp. F in dorsal and ventral views (a-b), and oronasal (c). CSIRO H5485.01 (516 mm DW; female; Kuching, Sarawak, Malaysia; photos by P. Last). Bars 10 cm (a-b), 10 mm (c).

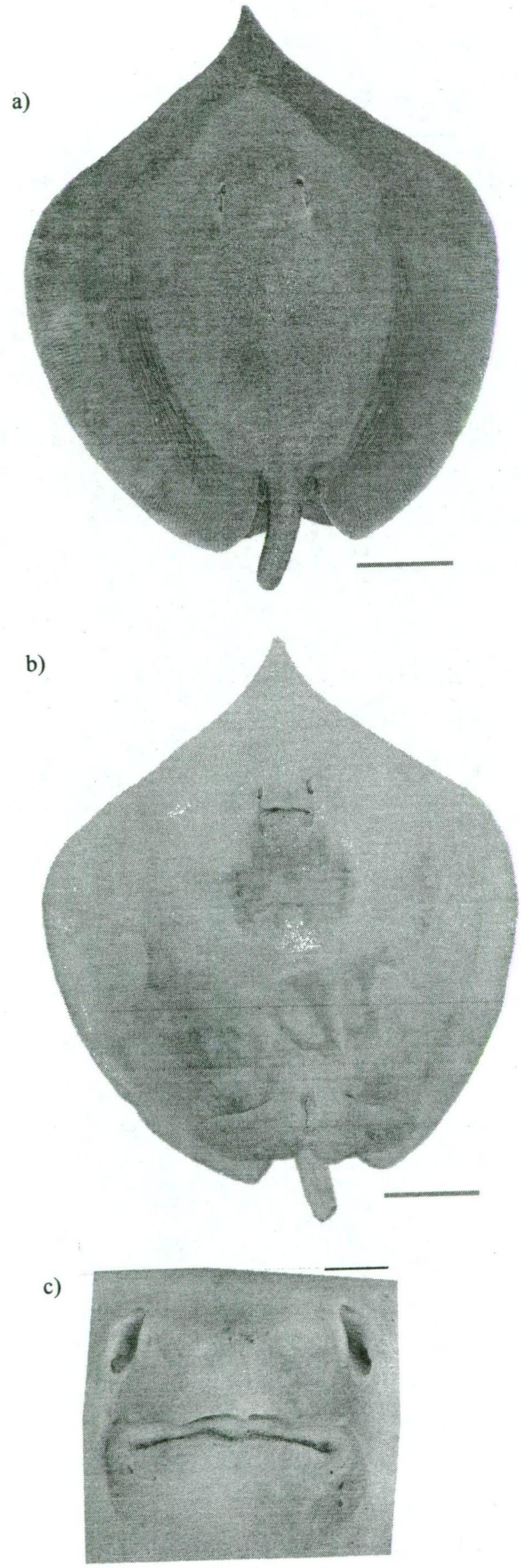
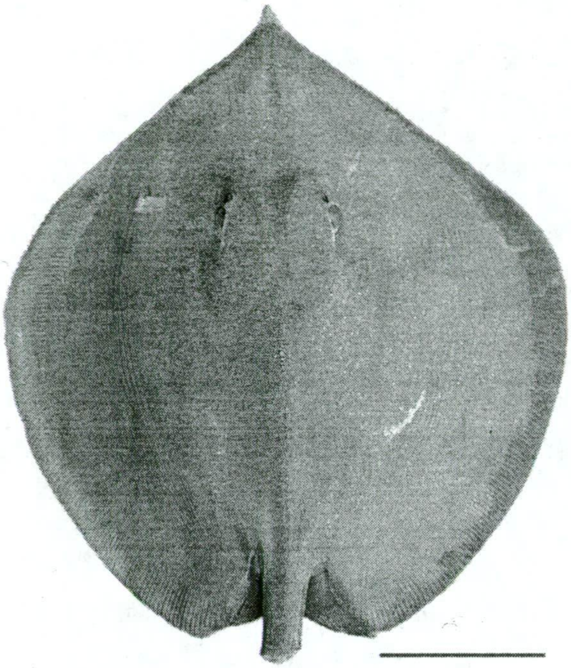
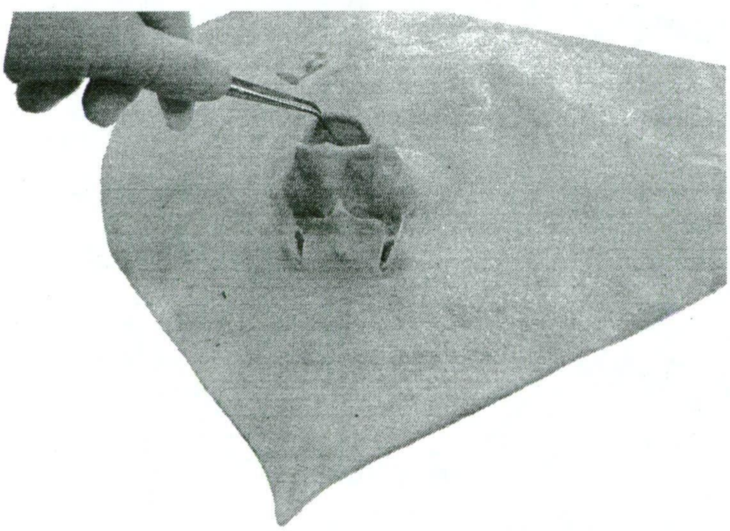

a)
b)
c)

Figure 5.3.14. Representative specimen of *Himantura* sp. F in dorsal view (a), and telescopic mouth (b). CSIRO H5472.01 (343 mm DW; female; Kuching, Sarawak, Malaysia). Bar 10 cm.

a)



b)



Skeletal morphology. — Neurocranium of 343 mm DW female (Figs. 3.2.7y, 3.2.8x) with moderately elongate and broad nasal capsules, anterior edge narrowly angular, broadly concave medially; nasal apertures transversely oval; fontanelle weak keyhole-shaped, extending far behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes short, knob-like; supraorbital crests low, slightly convex along orbital margin; sphenopterotic ridge a narrow ledge with straight margins, without any processes; lateral commisure moderately broad.

Scapulocoracoid (Fig. 3.2.10u) relatively broad, moderately high, posterior part strongly extended in lateral view; lateral face subtriangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; two small postdorsal foramina; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5 times as high as long; mesocondyle long and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11u) broadly arched, relatively thin, median prepelvic process absent, a pair of distinctive spatula-like anterolateral processes, moderately long dorsal iliac processes, and broadly rounded mesial ischial processes.

Morphology of clasper in adult male unknown.

Size. — Birth and maturity sizes unknown. The largest specimen, 516 mm DW female is probably maturing. Female specimens measuring about 1m disc width have been observed at fish markets in Sarawak.

Etymology. — Nil.

Common name. — Tubemouth whipray, in allusion to its protrusible tube-like mouth.

Distribution. — Known from Sarawak (southwestern Borneo) in the southern sector of the South China Sea. However, despite intensive field and market surveys across Borneo, particularly in the more northerly Malaysian state of Sabah (Fowler *et al.* 1999, pers. observations), this species has not been collected north of Bintulu, central Sarawak. Recent reports in 2003, of sightings supported by photographic evidence (communicated to Dr. P. Last), indicates that the species is found in southern Sumatra, Indonesia. It appears to be a coastal marine species found in association with runoff from large rivers.

Comparisons. — *Himantura* sp. F is categorized under the '*uarnacoides*' complex comprising five other species, *H. chaophraya* Monkolprasit & Roberts, *H. granulata* Macleay, *H. pastinacoides* (Bleeker), *H. uarnacoides* (Bleeker), and another undescribed long-snouted whipray from Papua New Guinea, *H.* sp E (this study). Important characteristics shared by members of this complex include a similar disc colour (uniform light to dark brown dorsally, and pale or whitish with or without a dark brown margin ventrally), a similar disc shape (pectoral apices very broadly rounded), and development of a plate-like denticle band on the dorsal surface of the disc. Within this complex, *H.* sp. F is most similar to *H.* sp. E, both having an extremely elongate snout (exceeding 35% of disc width compared with 26-35% in *H. chaophraya*, 20-26% in *H. granulata*, 18-23% in *H. pastinacoides*, and 24-29% in *H. uarnacoides)*, and very small eyes (3-5% of snout length compared with 5-8% in *H. chaophraya*, 14-30% in *H. granulata*, 18-23% in *H. pastinacoides*, and 10-16% in *H. uarnacoides). Himantura* sp. F differs from all other members of the subgroup by its extremely protrusible mouth and a pair of greatly enlarged lateral prepelvic processes on its pelvic girdle. This species is further distinguished from *H. chaophraya* by its more angular disc and more anteriorly expanded snout.

Remarks. — The smalleye stingray, *Dasyatis microphthalma* Chen, 1948, is known only from the unique holotype collected at the Keelung market, Taiwan. Although it was described as a *Dasyatis*, Chen's somewhat inadequate description of the holotype notes the lack of a ventral cutaneous skin fold on the tail which is typical of *Himantura* species. Hence, it was initially suspected as being conspecific with *H.* sp. F based on its gross morphological similarity (long snout and very small eyes), overlapping regional distribution, and the lack of additional recorded specimens of anything similar since its description more than 50 years ago. A thorough search for the holotype (by the student) at the two cited candidate repositories (Taiwan Museum and the Zoological Department of the National Taiwan University) was unsuccessful. It is now confirmed that the type is missing, presumed lost, and *D. microphthalma* considered a *nomen dubium*, possibly conspecific with *Dasyatis acutirostra* Nishida and Nakaya, 1988, whose types were collected from near Taiwan.

Chen compared his newly described species with two other dwarf stingrays that he considered as most closely related, i.e. *D. imbricatus* [note: *Himantura imbricata* (Bloch & Schneider, 1801)] and *D. walga* [note: *Himantura walga* (Müller & Henle, 1841)], and argued that *D. microphthalma* differed from these species by having a smaller eye, longer tail, and the presence of a thin skin fold on the floor of the mouth.

Differences in size between *D. microphthalma* and both *H. imbricata* and *H. walga* were also noted. The lengths at first maturity for males of the dwarf *Himantura* species are approximately 210 and 150 mm DW respectively, and maximum disc widths approximately 300 mm. On the other hand, the holotype of *D. microphthalma*, with an estimated size of 269 mm DW, based on the illustration accompanying the species description, is still immature (male), and thus is likely to well exceed 300 mm DW as an adult.

Chen's species was subsequently recognised as valid within *Dasyatis* (e.g. Chu 1960, Chu *et. al.* 1963, Chu & Wen 1979, Chen & Joung 1993, Shen 1993) and *Himantura* (Compagno & Roberts 1982). However, while some of these references reproduced Chen's original illustration, none actually produced a photograph of the holotype, or other convincing evidence that they had positively identified the species. Compagno (pers. comm. 1999) confirmed he has never seen a specimen of *D. microphthalma*, and mentioned of having doubts about its placement in

Himantura, partly because it also looked rather like the long-snouted *Dasyatis zugei*. However, based on a supposed 'lack of tail folds' in Chen's original description, Compagno assigned it to *Himantura*.

A comparison of the sensory pore patterns between a stingray specimen identified as *D. microphthalma* and *D. zugei* (Chu & Wen 1979), clearly indicate differences that are sufficient to support the two as different species. In *D. microphthalma*, the outer subpleural loop is shaped like a 'foot' (shaped like the number 3 in *D. zugei*), and the infraorbital canal extends toward the third gill slit (terminating at anterior of the first gill slits).

Further communication with researchers from Taiwan (K.M. Liu; H.-C. Yang) and Japan (H. Ishihara; K. Matsuura; G. Shinohara) led to the examination of two of the paratypes of *D. acutirostra*. This species is a marine stingray, with type localities from the East China Sea and southern part of Japanese waters, which are close to the presumed type locality of *D. microphthalma*. The two types (HUMZ 107588 and HUMZ 107591, 296 and 351 mm DW, the former an immature male and latter a female) are almost entirely smooth on the dorsal surface, except for 3 blunt conical denticles mid-disc of the larger specimen, and numerous minute spinulose denticles on the tail of both specimens. Chen described the holotype of *D. microphthalma* as 'having a smooth skin, with two round tubercles in middle of back, a patch of small asperities above before spine and also behind the spine along the upper and lateral surface of the tail to its extremity.' A fully developed plate-like denticle band is evident in both the specimens of *H.* sp. F (343 and 516 mm DW), the smaller specimen slightly smaller than the larger *D. acutirostra* paratype, and only about 7 cm bigger than the estimated size of *D. microphthalma*. It is further noted that a very short, ridge-like ventral tail skin fold, is present on both paratypes of *D. acutirostra* examined. Thus, it appears likely that, although Chen specifically mentioned that the tail of *D. microphthalma* lacked a skin fold, he may have overlooked this inconspicuous character, which is located directly below the sting, and measures approximately 1 mm in maximum height and 27-55 mm in base length. Moreover, the tail length of *D. microphthalma*, which was described as 'one and a half times the length of the body', is similar to that of *D. acutirostra* (1.58-

1.63 times). Comparison of morphometric ratios further support that *D. microphthalma* is more similar to *D. acutirostra* than to *H.* sp.F. Chen described the disc shape of *D. microphthalma* as 'disk as broad as long'; the proportional measurement of disc width over disc length for *D. acutirostra* is 97-98% and *H.* sp. F 88-90%.

Elsewhere in the region, an image of a stingray resembling a large *H. uarnacoides* or *H.* sp. F from Indonesia was published erroneously in Djamali *et al.* (1994) as *Himantura uarnak* (Forsskål 1775). The authors used stingrays as an example of 'toxic and poisonous marine fishes of Indonesia', and gave a brief description of the illustrated species as, '... Tail very long and with multiple long black lines. Disc shape resembling that of a kite with rounded corners. It is called Sandy Stingray because of its sand-like colour, i.e. dark brown.' The most recent but still unconfirmed report of the occurrence of *D. microphthalma* is from the Nan River in Thailand by Wongrat (1998). The author reported an unidentified *Himantura* with a disc shape similar to *H. microphthalma* as given in Figure 1 of Compagno and Roberts (1982), but did not elaborate.

NOTE: Since the writing of this section, several more specimens have been collected from the same locality, as well as other localities nearby. The new information is incorporated in the species description to be published.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

CSIRO H5472.01[e], CSIRO H5485.01 (Kuching, Sarawak, Malaysia).

5.4 'SIGNIFER' COMPLEX

5.4.1 Definition

Small species, adults not exceeding 300 mm in disc width (except in *H. oxyrhyncha*, maximum disc width reaching to 360 mm). Disc shape oval; snout angular at tip; lateral apices broadly to evenly rounded; tail stout and short (in *H. imbricata*), broad-based and whip-like (in *H. signifer* and *H. walga*), slender and whip-like (in *H. oxyrhyncha* and *H.* sp. G). Dorsal surface of disc generally plain coloured (brownish polygonal spots and/or reticulations present in *H. oxyrhyncha*); ventral surface plain and pale. Tail plain (uniform) coloured, upper half of dorsal surface darker than lower half. Teeth sexually dimorphic, cusps of mature males acute and elongate. Row of enlarged denticles along trunk and midline of tail present. Two stinging spines usually present, third sting often present.

5.4.2 Key

1 Denticle band well developed by 200 mm disc width **2**

Denticle band not well developed by 200 mm disc width **5**

2 Upper surface of disc diffuse with dark polygonal spots usually confined along trunk (rarely plain coloured); independent row of enlarged heart-shaped denticles along mid-trunk to mid-line of the tail present, crowns elevated above skin ... ... ***Himantura oxyrhyncha* (p. 5-257)**

Upper surface of disc plain (uniform colour) **3**

3 Midscapular denticle pearl-shaped; independent row of enlarged heart- to spear- shaped denticles along mid-trunk from above mid-first synarcual to sting base present ... ... ***Himantura* sp. G (p. 5-295)**

Midscapular denticle small, seed-shaped; independent row of small and large thorns along mid-line of the tail present, crowns convex, free posterior tip extended from base **4**

4 Dorsal and ventral keels, and/or rudimentary ventral fold present; cross-section of tail at sting base more or less quadrangular; mature females without club-like tail ... ... ***Himantura imbricata* (p. 5-245)**

Dorsal and ventral keels and/or rudimentary ventral fold absent; cross-section of tail at sting base compressed; mature females often with club-like tail tip ... ... ***Himantura walga* (p. 5-278)**

5 Upper surface of disc uniform plain gray; presence of independent rows of enlarged flat heart-shaped denticles along midline on posterior half of abdomen to sting base ... ... ***Himantura signifer*** **(p. 5-269)**

Himantura imbricata (Bloch & Schneider 1801)

Scaly whipray

Figures 3.2.9c, 5.4.1-5.4.2; Tables 5.4.1-5.4.2

Raja imbricata Bloch & Schneider 1801: 366, 553 (original description based on a mature male specimen, no designated type). Holotype: ZMB 7585 (dry mounted), 125 mm disc width (measurement by P. Last), mature male. Type locality: mouth of the Coromandel, India.

Synonymy. —

Trygon dadong Bleeker 1856: 355 (original description based on a female specimen 163 mm disc width, not figured). Possible holotype: RMNH 7446, 158 mm disc width (measurements by P. Last). Locality: Indonesia (Rio and Bintang).

Trygon imbricatus: Blyth 1860, 40 (brief description). Locality: Lower Bengal.

Trygon (Himantura) polylepis (not Bleeker): Günther 1870, 475 (brief description based on skin of an adult male from Dr. Kelaart's collection in the British Museum). Locality: Ceylon.

Trygon (Trygon) imbricata: Günther 1870, 481 (brief description). Locality: Indian seas.

Leiobatis (Himantura) dadong: Bleeker 1877, figs. 1a and 1b, pl. 557, Plagiostom. Pl. 35 (illustration of holotype).

Dasybatus (Himanturus) imbricatus: Garman 1913, 379 (description, misidentification in part). Locality: East Indies.

Dasyatus (Amphotistius) imbricatus: Fowler 1956, 43 (brief description, misidentification in part). Localities: Red Sea and Southern Arabia.

Dasyatis (Amphotistius) imbricata: Chandy 1957 (in-depth anatomical study). Locality: India.

Himantura imbricata: Compagno & Roberts 1982, 325 (listed).

Dasyatis imbricata: Dor 1984, 17 (listed). Locality: Red Sea.

Amphotistius imbricatus: Rainboth 1996, 52 (misidentification in part). Locality: Cambodian Mekong.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape oval; preorbital snout long, broadly concave, with a distinct apical lobe; anterior disc margin strongly concave, lateral apices evenly rounded, posterior margin almost straight rather than evenly broadly rounded. Dorsal surface of disc uniform dark brownish, with paler disc margins; ventrally pale (whitish), with darker disc margins; tail uniformly dark brownish on dorsal half, and on entire surface behind tip of stings; ventral half pale whitish. Secondary median denticle band developed along sub-primary denticle band, and independent row of enlarged denticles on tail between tail base and sting base; width of secondary band confined to a narrow median band along trunk, not exceeding interspiracular width, constricted at nape adjacent subprimary denticle band in front of suprascapular denticle.

Description. — Disc oval, width 0.90-0.98 in length; robust, center raised at mid-scapular, maximum disc thickness 0.10-0.13 in disc width (DW); preorbital snout long, broadly concave, with a distinct apical lobe, angle 106.5-115°; anterior margins of disc strongly concave, lateral apices evenly rounded; posterior margin almost straight rather than evenly broadly rounded, free rear tip narrowly rounded (Figs. 5.4.1-5.4.2). Pelvic fins moderately long, 19.8-21.9% DW; width across base 13.0-16.3% DW. Claspers of adult male short and stout, dorsal and ventral surfaces slightly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle long, about 2/3rd of clasper length on its outer margin, weak notch anteriorly. Tail stout and short, length 0.85-0.87 times disc width; base depressed, subcircular in cross-section, width 1.40-1.70 times height at base. Rudimentary skin fold present (Fig. 5.4.1d).

Snout long, depressed; preoral snout length 3.62-4.13 times mouth width, 2.29-3.29 times internarial distance, 27.2-34.1% DW; direct preorbital snout length 2.20-3.03 times interorbital length, horizontal length 2.11-2.94 times interorbital length; snout to maximum disc width 42.1-50.5% DW; interorbital space slightly convex; eye moderately large, diameter 54-93% spiracle length; orbits slightly protruded, diameter 0.99-1.49 in spiracle length, interorbital distance 1.51-2.04 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, weakly laterally expanded, outer margin with a weak concavity, length 0.34-0.46 in internasal distance; internasal distance 0.37-0.55 of prenasal length, 2.20-2.94 times nostril length. Nasal curtain subrectangular-shaped, relatively broad, width 1.64-1.98 times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2 well-developed papillae (a small 'knob-like' papillae between the two present in one specimen), rounded distally (sometimes bifurcate), longitudinally flattened, sub-equal in size, located near to each other.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, mature males with pointed (sharp) peak. Tooth row count not available.

Gill opening margins smooth, straight; length of first gill slit 1.27-1.70 times length of fifth, 0.24-0.41 of mouth width; distance between first gill slits 1.77-2.24 times internasal distance, 0.38-0.44 of ventral head length; distance between fifth gill slits 1.13-1.44 times internasal distance, 0.24-0.28 in ventral head length.

Squamation. — Stages of squamation with narrow overlapping size ranges; with Stages 1-3 including tail denticles simultaneously developing. Secondary denticle band a narrow, continuous longitudinal band with well-defined margins, constricted at nape.

Holotype is in early part of Stage 4: its dorsal surface with a developed primary denticle band, and developing secondary median denticle band; outside of band, skin smooth, without denticles. Secondary band narrow, confined to a few irregular rows adjacent primary band, head and scapular patches weakly interconnected at nape. Band extended to interorbital, posteriorly continuing on to tail to sting base; slightly expanded laterally at scapular, otherwise evenly wide along trunk.

Denticles in band flat narrow heart-shape, closely-set; subequal in size. A prominent narrow heart-shaped suprascapular denticle.

Stage 0: from birth (ca. 100 mm DW) — Disc entirely smooth; a small narrow heart-shaped suprascapular denticle (length 1.7-3.5 mm) appearing during late part of this stage.

Stages 1-3: (ca. ?110 mm DW) — The question mark denotes the likely size for this stage, as there is no representative specimen available for study; the holotype at 125 mm DW (measurement by P. Last) is in Stage 4.

Development of primary, median denticle band above first synarcual seemingly simultaneous with the initial development of discontinuous secondary denticle patches on head and scapular, and independent row of enlarged denticles on tail between tail base and sting base.

Primary band developing as a single row of enlarged denticles, consisting of seed-shape to narrow heart-shape thorns; smaller than suprascapular denticle. Secondary denticle patch above head loosely-set, smaller than those above scapular; denticles above scapular more closely-set, almost abutted. Enlarged denticles along midline of the tail consisting of small and large thorns with convex crowns, free posterior tip extended from base, dorsoposteriorly projected; those anteriorly smaller, closely-set, almost abutted, others uniformly spaced between each other (space equal to length of one of the preceding thorns); length of largest almost two times length of smaller ones; posteriormost thorn with bifurcate base.

Stage 4: (ca. 120 mm DW) — In early part of this stage, cranial and scapular denticle patches coalesced to form an irregular longitudinal band; primary denticle band becoming weakly evident.

Late stage four (>150 mm DW), secondary median denticle band well-developed as a narrow, continuous longitudinal band with well-defined margins, constricted at nape adjacent subprimary denticle band, in front of suprascapular denticle. Band extending to just in front of orbits; naked snout ratio 81.1-85.4%; width confined to a narrow median band along trunk, not exceeding interspiracular width, gradually narrowing a short distance above abdomen, becoming almost as wide as tail width at pectoral-fin insertion, before extending on to tail adjacent enlarged denticles midline of tail to sting base.

Denticles largest along median line, decreasing towards lateral margins of band; smaller denticles interspersed among larger ones.

Stages 5 and 6 not applicable for this species.

Two elongate stinging spines usually present, a third sting sometimes present.

Meristics. — Total pectoral-fin radials 106-108 (n=3); propterygium 46-49, mesopterygium 13-17, metapterygium 44-46; pelvic-fin radials 19-26 (n=3); vertebral segments 91-99 (n=3), monospondylous 37-38, prespine diplospondylous 43-51, and postspine diplospondylous 4-11.

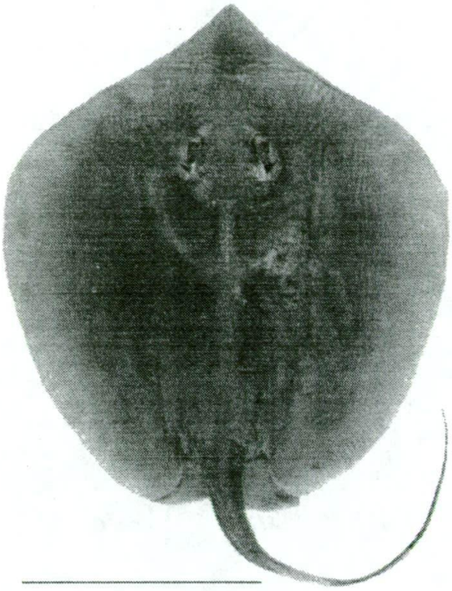
Colour. — In fresh, disc uniform dark brownish, with paler disc margins; ventral disc uniform pale (whitish), with darker disc margins. Tail uniformly dark brownish on dorsal half, and on entire surface behind tip of stings; ventral half pale whitish.

Skeletal morphology. — No dissections were carried out. However, based on x-ray plates, the shape of the neurocranium is of a 'typical' *Himantura*.

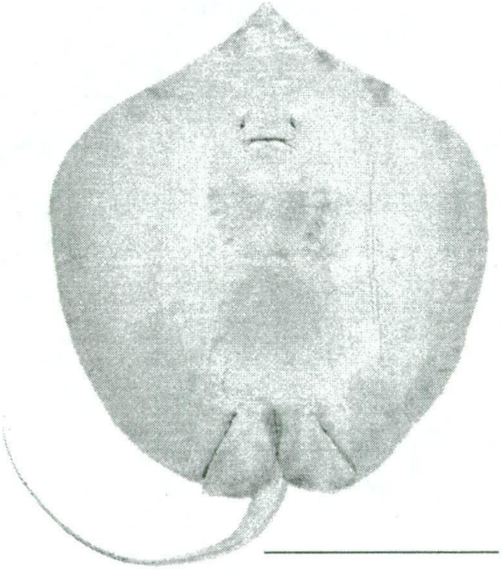
Size. — Birth size around 100 mm DW; length at first maturity (males) between 205 and 210 mm DW. A 203 mm DW male specimen (LACM 38130-60[4of10]) was determined as being an immature (maturity stage 2), while two males (LACM 38130-60[1of10] and LACM 38130-60[2of10]) 214 and 232 mm DW respectively, as mature (maturity stage 4). Largest female examined 207 mm DW (LACM 38134-37[1of2]) is probably maturing. Maximum disc width 300 mm (Compagno & Heemstra 1984).

Figure 5.4.1. Representative specimen of *Himantura imbricata* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, oronasal; d, rudimentary ventral skin fold on tail. NTM S.13160.009 (188 mm DW; female; Chilaw, Sri Lanka; photos by T. Carter). Bars 10 cm (a-b), 10 mm (c).

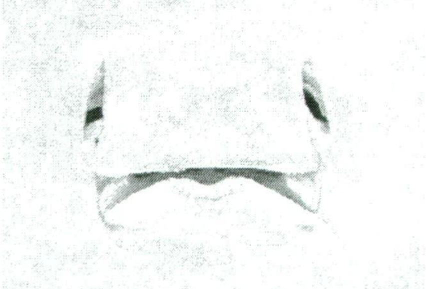
a)



b)



c)



d)

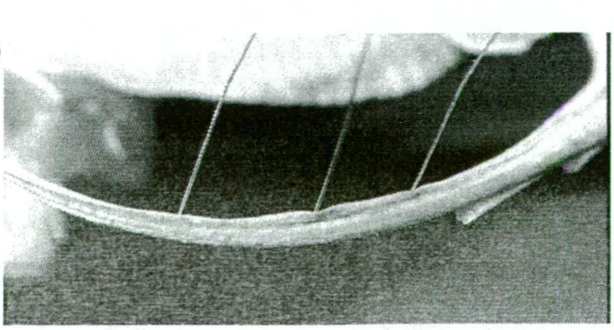
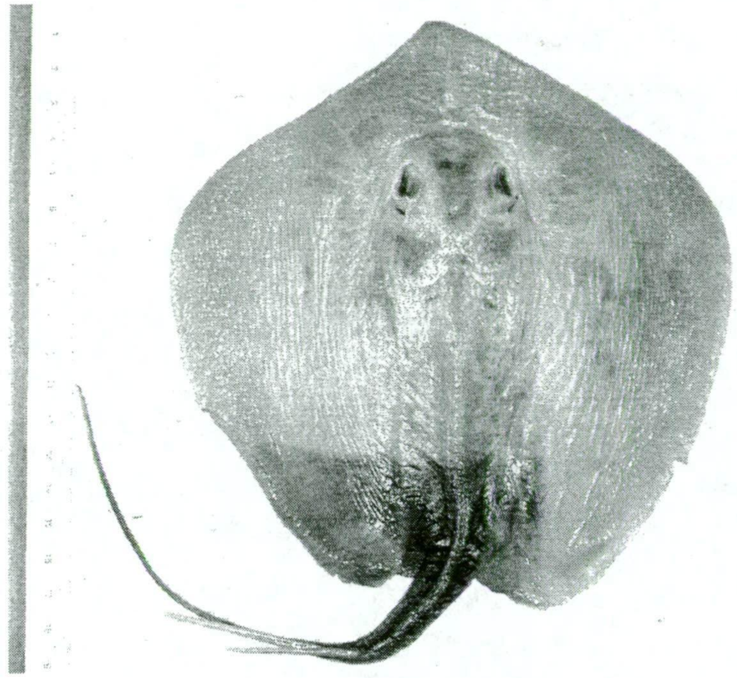
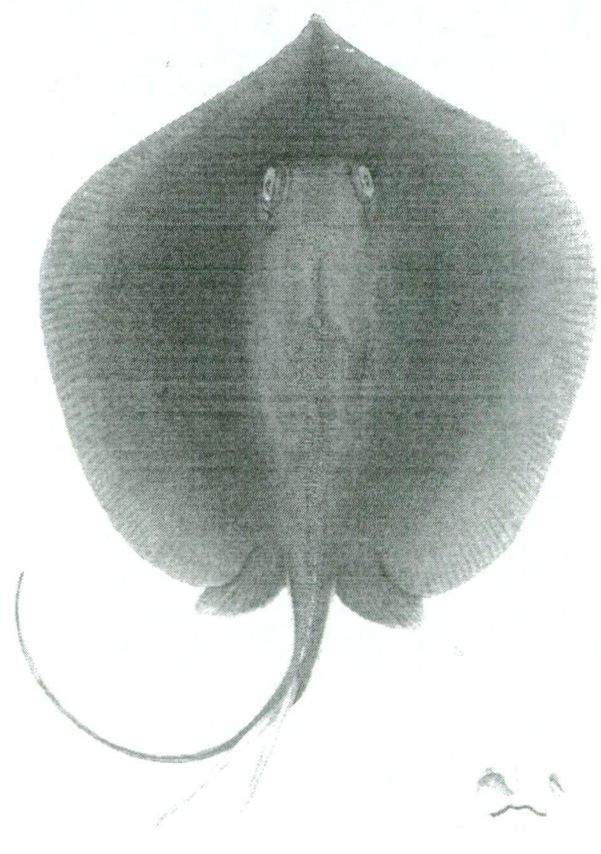


Figure 5.4.2. Holotype of *Trygon dadong* in dorsal view. a, RMNH 7446 (158 mm DW; female; Bintang, Indonesia; photos and measurements by P. Last); b, illustration (reproduced from Bleeker 1877: fig. 1, pl. 557, Plagiostom. Pl. 35).

a)



b)



Etymology. — Not specified. However, Rob Kelly (pers. comm. 2000) who helped translate the Latin text into English, noted that *imbricata* is a word formed from 'imbrix' which is a special type of concave roof tile; suggesting this must have been used to describe the tile-like 'scales' or 'plates' on the (dorsal surface of the) stingray.

Common name. — Scaly whipray (Last & Compagno 1999)

Distribution. — Red Sea; India (shore area, Coromandel coast; lower Bengal), Indonesia (Java) (e.g. Bleeker 1856; Blyth 1860; Chandy 1957; Dor 1984).

Comparisons. — *Himantura imbricata* is very similar with *H. walga*, particularly in general disc shape, but their geographical distribution appear limited and almost non-overlapping (P. Last pers. comm.). The former is apparently found only in the Indian Ocean, the latter in the South China Sea.

Himantura imbricata and *H. walga* may be distinguished by a combination of two characters, i.e. the shape of their tail and rate of squamation. On the other hand, two forms of *H. imbricata* is herein recognized, also based on the morphology of the tail. These are tentatively termed 'Kuwait sandwich-tail' and 'Pakistan sandwich-tail', i.e. dark brown on dorsal and ventral surfaces, and white in-between, hence 'sandwich-tail'.

In both sandwich-tail forms and *H. walga*, a longitudinal keel along the ventral surface is present. However, these differ in cross-section outline shape, i.e. ventrally medially sloped in *H. imbricata* (Kuwait and Pakistan specimens) versus ventrally double convex and the medial groove with prominent longitudinal ridge in *H. walga* (Thailand specimen).

As for denticle development, the rate is faster in *H. imbricata* (Pakistan sandwich-tail) compared with *H. walga* (Borneo).

Comparing the two *H. imbricata* sandwich-tail forms, the tail is slightly darker on the dorsal surface than on the ventral surface in Kuwait sandwich-tail. Pakistan sandwich-tail have a uniform dark colour on both dorsal and ventral surfaces of the tail, although slightly paler on the ventral keel.

Remarks. — *Raja imbricata* Bloch and Schneider (1801; see Karrer *et al.* 1994 for suggested authorship of species and translation of introduction) was described without any type specimen being designated. However, an example of a male specimen with size just over one foot long (ca. 305 mm) was mentioned, and that it was from Coromandel, India.

Eschmeyer (On-Line, ver. February 15, 2002) later lists ZMB 7585 as the holotype of *H. imbricata*, a dry specimen and the locality as from Tranquebar, India. This specimen was examined by P. Last (pers. comm.), but on the label of the specimen it was written 'Coromandel', which is most likely its locality. With regards to measurements, Bloch and Schneider's statement about the length is unclear. Nevertheless, based on Lasts' estimation (pers. comm.) of the 'total length', 'disc width', and 'disc length' of this specimen, they probably referred to the total length (i.e. 310 mm); the other two measurements are 125 mm disc width and 150 mm disc length.

Photographs (courtesy P. Last) of the specimen indicate a dry mounted mature male specimen with most of the disc edge and part of the trunk chipped. The pectoral fin is torn apart from the trunk at pectoral-fin insertion, and stretched anteror-laterally, so that the disc length appears longer than it actually is. A denticle band extends along a narrow line mid-trunk, widest anteriorly and gradually narrowing posteriorly, anterior-most edge extends interorbitally, and posterior-most edge to base of first sting; denticles heart-shaped, uniform size, midscapular denticles seed-shaped, similar denticle shape also present at tail base. Thus it fits Bloch and Schneider's description where it was stated '*in one male example, little more than a foot long, small bony swellings, flat almost conical on the top of the head and arranged throughout the entire mid-spine of the back; on the head and in front of the larger serrated stings and almost like tiles, with the apices of several of the* *longer bones flat, or bent'* (as translated from Latin text by Rob Kelly, pers. comm.).

Apart from the holotype, the Sri Lankan female non-type (NTM S.13160.009; Fig. 5.4.1) is the only comfirmed *H. imbricata* specimen examined. The posterior margin of the disc is rather almost straight than sloping.

On synonymy, *Trygon dadong* Bleeker 1856 is herein considered a junior synonym of *H. imbricata*, based on examination of the holotype (RMNH 7446; Fig. 5.4.2a) by P. Last (pers. comm.), and the illustration in Bleeker's (1877) ichthyological atlas (Fig. 5.4.2b).

The validity of numerous other nominal taxa particularly those published during early last century, and which others have synonymized as *H. imbricata* (e.g. Garman 1913: *Isacurrah tenkee* Russell 1803, *Tenkee shindraki* Russell 1803, *Pastinaca dorsalis* Swainson 1839), could not be checked nor validated as these were either not accessible or that the full citation is not available despite efforts to locate these. Moreover, Last and Compagno (1999) in their species description for *H. walga* suggested that records of *H. walga* in the Indian Ocean might be *H. imbricata*, due to the confusion with this species.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

BPBM 33199(1of2), BPBM 33199(2of2) (Kuwait); CAS 141045 (mouth of Ganges River, India); LACM 38129-83(1of3), LACM 38129-83(2of3), LACM 38129-83(3of3), LACM 38130-60(1of10), LACM 38130-60(2of10), LACM 38130-60(3of10), LACM 38130-60(4of10), LACM 38314-24, LACM 38134-37(1of2) (Pakistan); NTM S.13160.009 (Chilaw, Sri Lanka); RMNH 7446[c] (holotype of *Trygon dadong*) (Bintang, Indonesia); ZMB 7585[c] (holotype) (Coromandel, India).

Himantura oxyrhyncha (Sauvage 1878)

Marbled whipray

Figures 3.2.1b, 3.2.6j, 3.2.7i, 3.2.8i, 3.2.9e, 3.2.10f, 3.2.11i, 5.4.3-5.4.4; Tables 5.4.3-5.4.4

Trygon (Himantura) oxyrhynchus Sauvage 1878: 91 (original description based on a female specimen, not figured). Holotype: MNHN 9639, 240 mm disc width. Type locality: Saigon, Cochinchine (=Cambodia).

Synonymy. —

Dasybatus (Himanturus) krempfi Chabanaud 1923a: 47, fig. 2 (original description based on three syntypes; oral papillae of one of the types figured). Syntypes: MNHN 1922-77, 136 mm disc width, immature male; MNHN 1922-78, 89 mm disc width, embryonic female; MNHN 1922-79, 117 mm disc width, immature female (measurements by P. Last). Type locality: Phnom Penh, Cambodia.

Dasybatus krempfi: Chabanaud 1923b, 558 (description of an adult female specimen, MNHN 1923-71, 350 mm disc width, not figured). Locality: Phnom Penh.

Dasyatis (Himantura) bleekeri (not Blyth): Suvatti 1981, 9, fig. 5 (listed, illustrated, misidentification). Locality: Thailand (Koh Yai, Chao Phraya River; Kwe Yai, Nan River).

Himantura krempfi: Compagno & Roberts 1982, 325, figs. 1D, 2, 3, 6C, 7B and 3D (redescription based on one of the syntype MNHN 1922-78 and non-type specimens, MNHN 1923-71 and an uncatalogued specimen). Locality of uncatalogued specimen unknown.

Himantura oxyrhyncha: Deynat & Fermon 2001, 163 (resurrection, redescription). Locality: Thailand (Menam Nan River), Cambodia (Phnom Penh, Mekong River).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: freshwater species; disc shape oval; preorbital snout long, strongly concave, with a distinct apical lobe; anterior disc margin strongly concave, lateral apices broadly rounded. Dorsal surface of disc and tail in young and adults diffused with irregular dark spots, ventrally white with dark grey disc margin, including posteror-lateral corner of nasal curtain gill slits, pelvic fins and ventral of tail base. Denticle band along mid-trunk sparse until about 500 mm disc width, mid-scapular denticle inconspicuous, thorns absent. Secondary denticle band rectangular-shaped, within which an independent row of enlarged heart-shaped denticles along mid-trunk from mid-disc to sting base is present.

Description. — Disc oval, width 0.85 (0.83-0.87) in length; flat, centre not raised at mid-scapular, maximum disc thickness 0.08 (0.10-0.13) in disc width (DW); preorbital snout long, strongly concave, with a distinct apical lobe, angle not available for holotype (96.0-100^{0}); anterior margins of disc strongly concave, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.4.3-5.4.4). Pelvic fins broad rectangular, long, 24.1% (23.7-26.7%) DW; width across base 15.8% (13.2-16.0%) DW. Mature male specimen not available for examination of clasper structure. Tail slender and whiplike, tapering gently toward sting, length 3.45 (3.00-3.58) times disc width; base narrow, subcircular in cross-section, width 1.28 (1.13-1.54) times height at base.

Snout long, depressed; preoral snout length 3.95 (3.20-4.81) times mouth width, 3.59 (2.90-3.73) times internarial distance, 36.0% (33.4-40.8%) DW; direct preorbital snout length 2.59 (2.24-3.05) times interorbital length, horizontal length 2.50 (2.08-3.03) times interorbital length; snout to maximum disc width 54.9% (51.0-63.4%) DW; interorbital space flat; eye moderately large, diameter 43% (44-63%) spiracle length; orbits slightly protruded, diameter 0.65 (0.71-1.03) in spiracle length, interorbital distance 3.17 (2.07-2.57) times orbit. Spiracles subrectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak concavity, length 0.43 (0.38-0.49) in internasal distance; internasal distance 0.33 (0.33-0.45) of prenasal length, 2.33 (2.04-2.64) times nostril length. Nasal curtain skirt-shaped, relatively broad, width 2.30 (1.65-2.04) times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor of holotype with 2-5 oral papillae in two transverse rows; medial pair (sometimes a third one present) rounded or trifurcate distally; outer pair located at each corner of mouth. In others (syntypes and nontypes of *H. krempfi*), consistently with four lobate papillae. Chabanaud (1923a) reported the oral papillae of the largest male syntype, as arranged in two transverse rows, but not in the younger specimens.

Teeth small, smaller in upper jaws; cone-shaped with blunt peak, with prominent horizontal groove. Tooth rows 42 (15-38) in upper jaw, 45 (24-38) in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.05 (1.04-1.61) times length of fifth, 0.31 (0.27-0.38) of mouth width; distance between first gill slits 2.25 (2.03-2.32) times internasal distance, 0.36 (0.33-0.38) of ventral head length; distance between fifth gill slits not available for holotype (1.40-1.59) times internasal distance, not available for holotype (0.23-0.28) in ventral head length.

Squamation. — Stages of squamation with narrow size ranges, with Stages 2 and 3 including tail denticles simultaneously developing.

Holotype is in late part of Stages 3 and 4 (Fig. 5.4.3): its dorsal surface with a well-developed secondary median denticle band, as a continuous bottle-shape longitudinal band with well-defined margin, within which an independent row of enlarged heart-shaped denticles along mid-trunk from mid-disc to sting base is present. Band extended from just anterior of orbits to the tail, very gradually narrowing posteriorly from level of scapular to tail base, evenly wide from tail base to sting base; outside of denticle band, skin smooth, without denticles. Denticles in band uniform flat narrow heart-shape, closely-set; size gradually decreasing towards band margin.

Stage 0: from birth (ca. 90 mm DW) (Fig. 5.4.4)— Disc entirely smooth; without any suprascapular denticles. In mid-part of the stage (ca. 110 mm DW), one ovate- to pearl-shaped denticle emerging under skin on suprascapular; two pearl-shaped denticles observed from photograph of a 158 mm DW immature male specimen (MNHN 1986-716). Supra- or mid- scapular denticles fully exposed by ca. 117 mm DW. Size (width) of the midscapular denticle 3.40 mm in holotype, ranging between 2.10-4.21 mm in others.

Stages 2 and 3: (ca. 120-135 mm DW) — Initial development of discontinuous secondary denticle patches on head and scapular region simultaneous with development of independent row of enlarged heart-shaped denticles along mid-trunk from mid-disc to tail sting base.

As the development progresses, more denticles appearing above the interorbital and adjacent to the enlarged denticles above the abdomen as weakly coalescing patches; longitudinal band margin weakly defined. Denticles uniform flat narrow heart-shape, widely-spaced with about 1-5 denticles apart.

Stage 4: (>150 mm DW) — Secondary median denticle band well-developed by ca. 158 mm DW, as a continuous subrectangular longitudinal band with a well-defined margin.

Specimens larger than 173 mm DW were not available to be personally examined in this study. However, based on the squamation description by Deynat and Fermon (2001), herein reproduced (emphasis in parentheses mine), squamation Stage 5 is applicable for this species: 'squamation in specimens (up to 345 mm DW), pectoral fins sparsely covered with very small denticles with stellate bases and blunt crowns, not modified into acuminate tip; small spiny denticles with stellate basal plate occur on the dorso-lateral sides of the tail, from posterior tip of sting to the tip of the tail, absent in smaller specimens; ventral surface of the disc and tail perfectly smooth.'

Stages 1 and 6 not applicable for this species.

Single elongate stinging spine present.

Meristics. — Total pectoral-fin radials (results given in the following order: range for holotype, three paratypes, and nontypes in parentheses; with n=4, number of nontype specimens examined; data for types as in Deynat and Fermon 2001): 118, 112-117 (116-121); propterygium 56, 53-57 (54-59), mesopterygium 15, 12-17 (14-18), metapterygium 47, 44-47 (46-47); pelvic-fin radials 26, 18-20 (22-29; n=4); vertebral segments 114, 112-119 (103-109)(n=4), monospondylous and diplospondylous data not available from Deynat and Fermon; monospondylous (34-40) (n=4), prespine diplospondylous (63-72) (n=4), and postspine diplospondylous 1-6 (n=3).

Colour. — Dorsal and ventral surfaces, including tail of holotype uniformly pale whitish (Fig. 5.4.3). However, Deynat and Fermon (2001) noted the presence of pale brown hexagonal blotches on its dorsal surface.

Fresh specimens uniform light brown, usually diffuse with dark irregular blotches along mid-trunk, extending from interorbital to sting base; remaining so, but becoming more conspicuous with age. In one specimen 158 mm DW (MNHN 1986-716), the entire dorsal disc surface covered with dark irregular blotches.

Skeletal morphology. — Neurocranium of 173 mm DW immature male (Figs. 3.2.7i, 3.2.8i) with short and rounded nasal capsules, anterior edge angular, broadly concave medially; nasal apertures transversely oval, internasal moderately broad; fontanelle subrectangular, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, just anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes small triangular, posteriorly pointed; supraorbital crests low and strong, uniformly wide along orbital margin; sphenopterotic ridge a narrow ledge with straight margins; lateral commisure moderately broad.

Figure 5.4.3. Holotype of *Himantura oxyrhyncha* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, midscapular denticles; d, tail base, indicating enlarged denticles along trunk continuing onto tail. MNHN 9639 (243 mm DW; female; Vietnam). Photos and measurements by P. Last. Bars 10 mm.

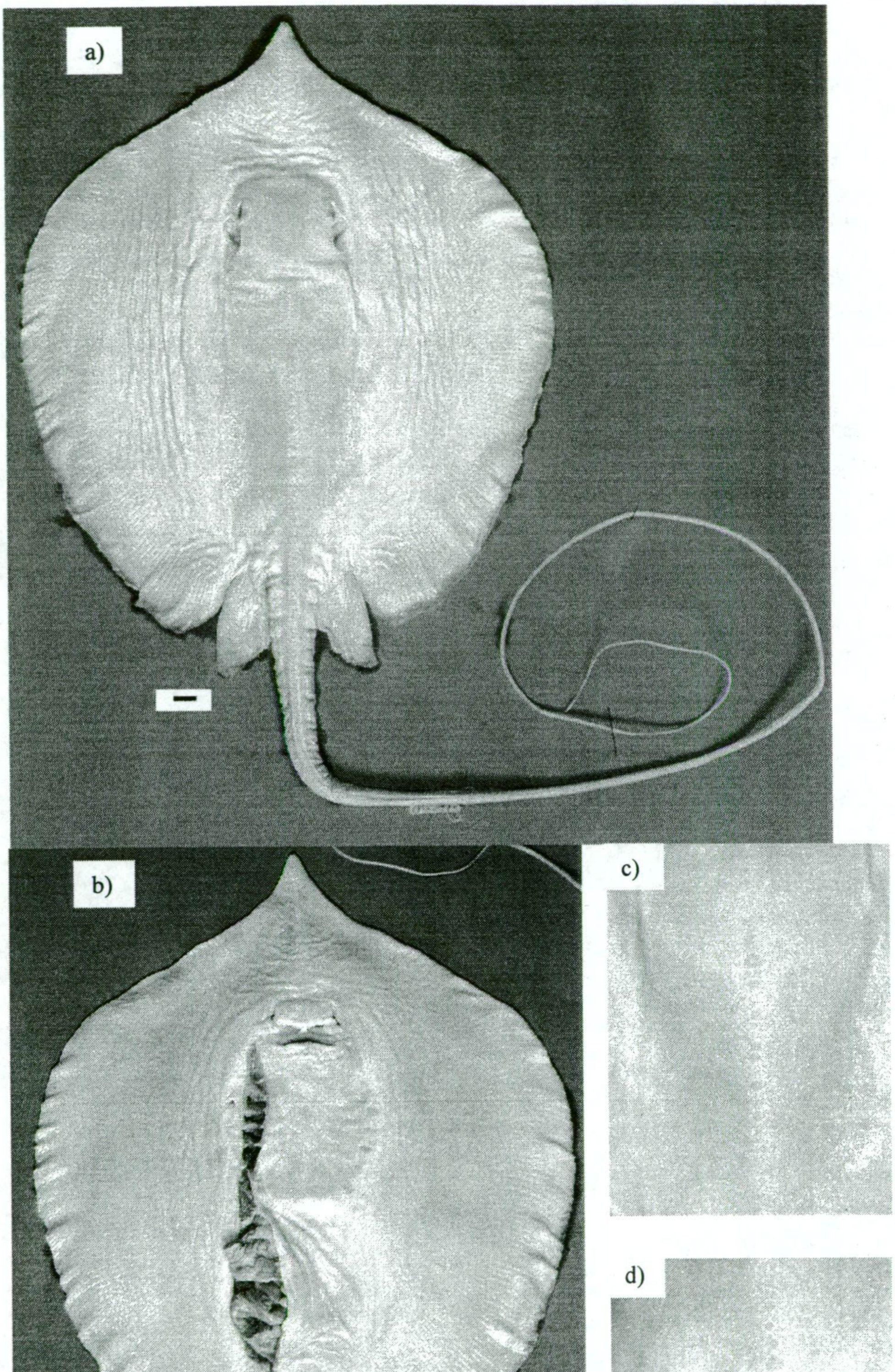
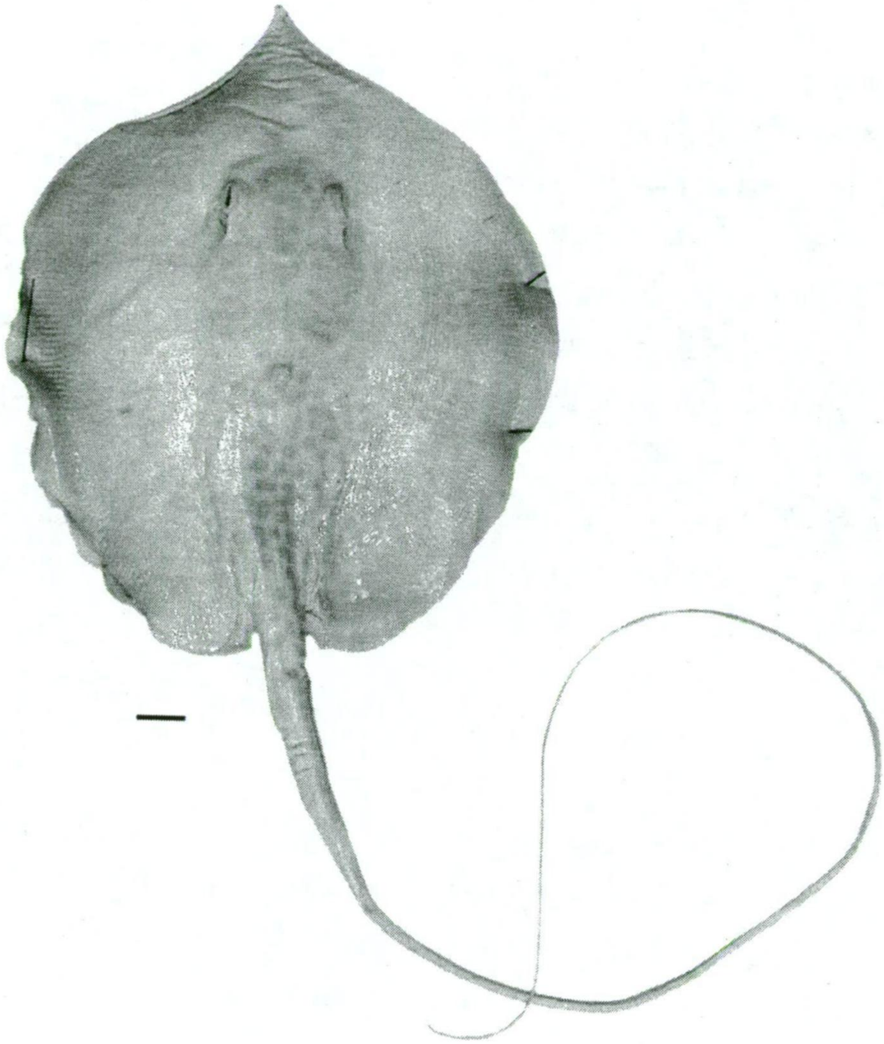

a)
b)
c)
d)

Figure 5.4.4. One of three syntypes of *Dasybatus (Himanturus) krempfi* in dorsal and ventral views. MNHN 1922-79 (117 mm DW; female; Vietnam). Photos and measurements by P. Last. Bars 10 mm.



Scapulocoracoid (Fig. 3.2.10f) relatively broad, moderately high, posterior part weakly extended in lateral view; lateral face subtriangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; two minute postdorsal foramina; fenestra on scapular process absent. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5-3 times as high as long; mesocondyle short and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11i) moderately arched, relatively thick, median prepelvic process present, small anterolateral processes, moderately long dorsal iliac processes, and narrowly rounded mesial ischial processes.

Mixopterygium of adult males unknown.

Size. — Birth size around 88 mm DW; length at first maturity unknown. The largest male specimen (ZRC 42984), 173 mm DW was determined as being an immature (maturity stage 2), whereas a female specimen 345 mm DW is also still immature (Compagno & Roberts 1982; specimen identified as *H. krempfi*). Maximum disc width 360 mm (Last & Compagno 1999).

Etymology. — Not specified, but Sauvage (1978) implied the name is based on the long and pointed snout, and presence of 'granulated' colouration on the dorsal disc surface.

Common name. — Marbled whipray (Last & Compagno 1999).

Distribution. — Saigon, Cochinchine (=Cambodia), Phnom Penh (Vietnam); Chao Phraya River, Koh Yai, Kwe Yai, Nan River, Menam Nan River (Thailand) (e.g. Sauvage 1878; Chabanaud 1923a, b; Suvatti 1981; Deynat & Fermon 2001); Kapuas Basin, Kalimantan (K. Lim, pers. comm.). Another report from freshwater in Daro, Sarawak, requires additional information to verify the record (unidentified correspondent via P. Last, pers. comm.); it is based on a colour photograph of a seemingly large specimen *H.* cf. *oxyrhyncha*.

Comparisons. — Comparison of the proportional measurements and counts for the holotype of *H. oxyrhyncha*, and syntypes of *H. krempfi* - two nominal freshwater species that have been confused with each other, and with other stingrays possessing dark colour patterns on the dorsal disc surface (i.e. *H. uarnak*) - as well as nontype specimens tentatively identified as either one of the two, indicated similar values, with overlapping values for both sexes (Tabs. 5.4.3-5.4.4).

On the other hand, *H. oxyrhyncha* may be easily distinguished from *H. uarnak*, based on disc shape, squamation, dorsal disc colouration and habitat. The disc of *H. oxyrhyncha* is oval-shape, disc longer than its width; an independent row of enlarged heart-shape denticles along mid-trunk from midscapular to sting base present in young and adults; and the species have only been recorded from freshwater.

Remarks. — It is noted that the disc width of the holotype of *H. oxyrhyncha* as measured by P. Last (pers. comm. 2001), is slightly longer than that given by Sauvage (1878), i.e. 243 mm DW vs. 240 mm DW. The range in number of tooth rows is also notably very wide, apparently increasing with age; however, no apparent trend was observed between sexes; nevertheless, it is expected that teeth shape of this species might display a sexual dimorphism, with adult males having teeth with sharp and pointed crowns, as observed in other members of the 'signifer' complex.

Compagno and Roberts (1982) recognized *H. krempfi*, and synonymized *H. oxyrhyncha* with *H. uarnak*. However, Last and Compagno (1999) later recognized both *H. krempfi* and *H. oxyrhyncha*. In their work, only a brief account of the latter was given, but nothing on the former, apart from it being listed; this rather reflect the lack of study material (P. Last pers. comm.).

Deynat and Fermon (2001) recently resurrected this species, after they re-examined its status based on comparison of morphological, squamation and disc colour characteristics between specimens of *H. krempfi* and *H. uarnak* in the Muséum

National d'Histoire Naturelle, Paris. The authors concluded that the syntypes of *H. krempfi* are juvenile forms of *H. oxyrhyncha*, thus considered the latter as the valid species, and the former as the junior synonym.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

MNHN 9639[c] (holotype) (Saigon, Vietnam); MNHN 1922-77[c], MNHN 1922-78[c], MNHN 1922-79[c] (syntypes of *H. krempfi*) (Phnom Penh, Vietnam); MTUF 30002 (Thailand); ZRC 42984[a], ZRC 42991, ZRC 42992[e] (Kapuas Basin, Kalimantan, Indonesia).

Himantura signifer Compagno & Roberts 1982

Pale whipray

Figures 3.2.6l, 3.2.7b, 3.2.8b, 3.2.9f, 3.2.10h, 3.2.11k, 5.4.5;

Tables 5.4.5-5.4.6

Himantura signifer Compagno & Roberts 1982: 333, figs. 1A, 4, 7A, 8, 9A-C and 10 (original description based on 7 type specimens, figured). Type specimens: MZB 3004, 294 mm disc width, immature female (holotype); MZB 3005, 280 mm disc width; CAS 48777, 289 mm disc width, adult male; USNM 229492, 279 mm disc width, immature female; MNHN 1981-1342, 312 mm disc width, adult male; RMNH 28800, 278 mm disc width, adult male; and BMNH 1981.11.16.1, 382 mm disc width, adult female. Type localities: West Kalimantan, Indonesia (holotype from mouth of Sungai Ketunggau near mainstream of Kapuas River; paratypes obtained at Sintang fish market); all obtained during July 1976.

Synonymy. —
Nil.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: freshwater species; disc shape oval, centrally moderately robust; preorbital snout long, apical lobe almost indistinct; anterior disc margin weakly concave; lateral apices evenly rounded. Dorsal surface of disc uniform greyish brown with a distinct white edge to the pectoral and pelvic fins, and sides of the tail anterior to the sting(s); ventrally, including ventral surface of tail uniform pale; tail uniformly greyish brown anterior to the sting(s); posterior to the sting(s), white with evidence of grey mottling. Denticle band along mid-trunk sparse; denticles small, flat heart-shaped denticles interspersed with scattered, small, conical denticles, mid-scapular denticle inconspicuous in large specimens; independent (1-2) rows of enlarged, flat heart-shaped denticles along midline of trunk and tail.

Description. — Disc oval, width 0.95-0.98 in length; moderately robust, centre slightly raised at mid-scapular, maximum disc thickness 0.10-0.11 in disc width

(DW); preorbital snout long, weakly concave, with an almost indistinct apical lobe, angle 114-117°; anterior margins of disc weakly concave, lateral apices evenly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.4.5). Pelvic fins long, 24.0-26.1% DW; width across base 14.2-16.4% DW. Mature male specimen not available for examination of clasper structure. The following account is based on Compagno and Roberts (1982): claspers of adult male short and stout, dorsal surface slightly flattened, ventral surface broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle relatively short, about 1/3rd of clasper length on its outer margin, prominent notch anteriorly. Tail broad-based, whiplike, tapering gently toward sting, length 3.43-3.82 times disc width; base depressed, subcircular in cross-section, width 1.23-1.46 times height at base.

Snout long, depressed; preoral snout length 4.17-4.72 times mouth width, 3.64-3.81 times internarial distance, 25.7-28.6% DW; direct preorbital snout length 2.31-2.60 times interorbital length, horizontal length 2.21-2.48 times interorbital length; snout to maximum disc width 46.5-47.8% DW; interorbital space slightly convex; eye moderately large, diameter 46-55% spiracle length; orbits slightly protruded, diameter 0.71-0.82 in spiracle length, interorbital distance 2.02-2.74 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils large, laterally expanded, outer margin with a weak concavity, length 0.58-0.63 in internasal distance; internasal distance 0.32-0.34 in prenasal length, 1.55-1.72 times nostril length. Nasal curtain skirt-shaped, relatively narrow, width 1.47-1.73 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, extending to chin. Mouth floor with 4-5 short, well-developed papillae; medial pair variably sized (sometimes absent), a pair of large paramedial papillae, and a pair of small lateral papillae opposite ends of dental band (Compagno & Roberts 1982).

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, mature males with pointed (sharp) peak. Tooth rows 14-15 in upper jaw, 18 in lower jaw. (Higher count by Compagno and Roberts [1982] attributed to different counting methods).

Gill opening margins smooth, straight; length of first gill slit 1.24-1.64 times length of fifth, 0.43-0.47 of mouth width; distance between first gill slits 2.79-2.93 times internasal distance, 0.39-0.41 of ventral head length; distance between fifth gill slits 1.81-2.02 times internasal distance, 0.25-0.28 in ventral head length.

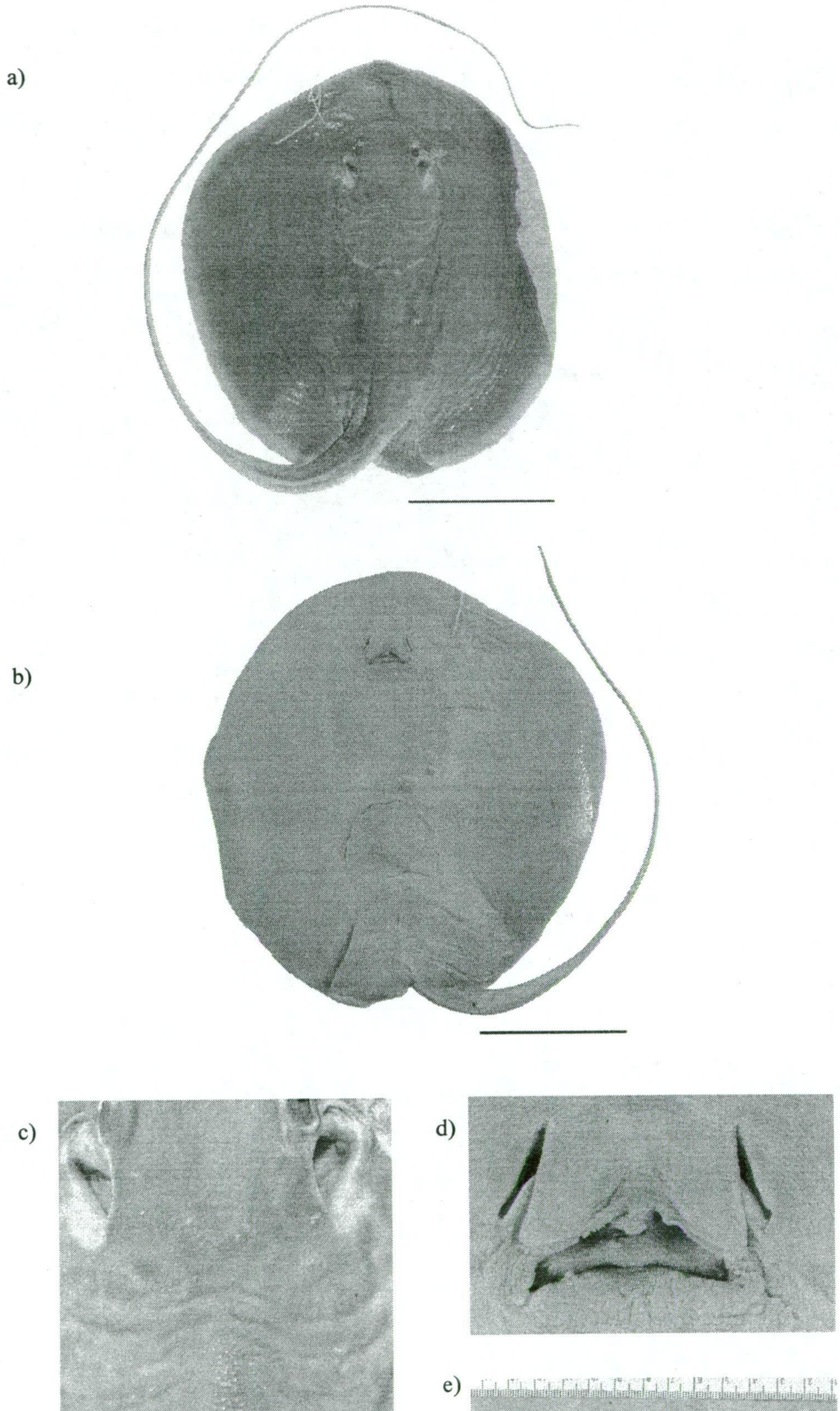
Squamation. — Stages of squamation with narrow overlapping size ranges; development of denticle band simultaneous with centre of disc appearing raised. Tail only sparsely covered with denticles.

Holotype is in Stages 3 and 4: its dorsal surface with a sparse median denticle band along the trunk from interorbital to tail base; denticles small, flat heart-shaped denticles interspersed with scattered, small, conical denticles with scalloped bases; denticles present on tail posterior to stings but absent on snout and lateral portions of disc; suprascapular denticle absent (Compagno & Roberts 1982: fig. 4).

Stage 0: from birth (ca. 110 mm DW) — Disc entirely smooth; a large ovate to pearl-shaped suprascapular denticle (3.36 mm) present, or only appearing during later stage (ca. 130 mm DW).

Stages 1-2: (ca. 240-270 mm DW) (Fig. 5.4.5) — Development of primary, median denticle band above first synarcual simultaneous with the initial development of discontinuous secondary denticle patches interorbital, around scapular and above the abdomen. Primary band developing in several irregular rows of closely-set of narrow heart-shaped denticles, whose bases are entirely embedded in skin. Secondary patches with weakly defined margins; denticles small, flat heart-shaped denticles interspersed with scattered, small, conical denticles.

Figure 5.4.5. One of six paratypes of *Himantura signifer* in dorsal and ventral views. a, dorsal disc; b, ventral disc; c, close-up of scapular denticles; d, close-up of oronasal (nasal curtain distorted); e, pelvic-fins and cloacal region. USNM 229492 (279 mm DW; female; Sintang, Kapuas River, Kalimantan, Indonesia). Photos by S. Raredon. Bars 10 cm.


a)
b)
c)
d)
e)

Stages 3-4: (ca. 250-280 mm DW) — Development of independent (1-2) rows of enlarged, flat heart-shaped denticles along midline on posterior half of abdomen, to sting base. Simultaneous development of cranial, scapular and abdominal denticle patches coalescing to form a regular longitudinal band. Number of denticles in band increasing, but remain widely spaced. Primary band and suprascapular denticle become inconspicuous. Secondary band with weakly defined margin.

Stages 5 and 6 not applicable for this species.

One to two elongate stinging spine present; two stings usually present.

Meristics. — Total pectoral-fin radials (results given in the following order: range for holotype and five paratypes as in Compagno & Roberts 1982, paratype USNM 229492, and nontypes in parentheses; with n=4, number of nontype specimens examined): 109-116, 111 (111-119); propterygium 50-54, 51-52 (50-54), mesopterygium 12-15, 13 (11-14), metapterygium 45-48, 46-47 (48-54); pelvic-fin radials 22-28, 27-28 (22-26); vertebral segments 109-116, 107 (105-107), monospondylous 34-41, 39 (34-30), diplospondylous data not available from Compagno & Roberts; prespine diplospondylous 59 (56-70), and postspine diplospondylous 9 (0-13) in paratype USNM 229492, and four nontypes respectively.

Colour. — In fresh, disc uniform greyish brown with a distinct white edge to the pectoral and pelvic fins, and sides of the tail anterior to the sting(s); white spots usually present anterior to eyes and just posterior of spiracles. A large female specimen, 328 mm DW (ZRC 40649) has small black spots on the dorsum (Tan & Lim 1998). Ventral disc including ventral surface of tail uniform pale. Tail uniformly greyish brown anterior to the sting(s); posterior to the sting(s), white with evidence of grey mottling.

Skeletal morphology. — Neurocranium of 252 mm DW female (Figs. 3.2.7b, 3.2.8b) with short nasal capsules, anterior edge broadly angular, slightly concave medially; nasal apertures transversely oval; fontanelle subrectangular, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, just anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes elongate and robust, rod-like throughout, posteriorly bluntly pointed; supraorbital crests low, slightly concave along orbital margin; sphenopterotic ridge a narrow ledge with a small pointed process; lateral commissure moderately broad.

Scapulocoracoid (Fig. 3.2.10h) relatively broad, moderately high, posterior part weakly extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a small postdorsal foramen; two minute fenestrae on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle high and long, 2.5-3 times as high as long; mesocondyle relatively short and broad, separated from metacondyle by deep notch; metacondyle half as long as procondyle.

Pelvic girdle (Fig. 3.2.11k) narrowly arched, relatively thick, median prepelvic process present, small anterolateral processes, long dorsal iliac processes, and narrowly rounded mesial ischial processes.

Mixopterygium of 289 mm DW male, as based on Compagno and Roberts (1982): relatively simple; 2 basal segments; beta cartilage not present as a separate element, apparently represented by a long, depressed, free cartilaginous flange originating anteriorly over basal segments and merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, subquadrate-triangular, with a truncate posterior edge, broad medial flange and narrow lateral flange that forms the roof of the clasper groove; ventral marginal cartilage narrow, laterally expanded plate on the axial cartilage, with a straight lateral margin forming the floor of the clasper groove; dorsal terminal cartilage large, broad, wedge-shaped, medially grooved, with a broad anterior base articulating with posterior edge of dorsal marginal, a narrow posterior end opposite tip of axial cartilage, and medial edge attached to axial cartilage; ventral terminal cartilage large, complex, oval-rectangular, and scoop-shaped, with a broad arched lateral flange forming the roof of the pseudopera and a recurved posterolateral tip forming a partial floor under it; terminal tip of axial cartilage not elongate, tip bluntly pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of mixopterygial tip, and narrowly extending to lateral surfaces.

Size. — Birth size around 110-115 mm DW; length at first maturity (males) around 210-230 mm DW, and around 250-260 mm DW for females (Tanaka & Ohnishi 1998). Three male specimens, 278, 289 and 312 mm DW, and a female specimen, 382 mm DW were determined as being adults, although the female holotype (294 mm DW) was determined as immature (Compagno & Roberts 1982).

Etymology. — According to Compagno and Roberts, the Latin epithet *signifer*, a noun, refers to the distinctive colouration (i.e. narrow white margin on the dorsal surface of the disc and sides of the tail anterior to the stings, and the tail posterior to the stings entirely white).

Common name. — Pale whipray (Last & Compagno 1999).

Distribution. — Thailand (Chao Phraya, Mekong and Tapi Rivers), Peninsular Malaysia (Sungai Perak), and Indonesia (central Sumatra and west Kalimantan) (e.g. Compagno & Roberts 1982; Roberts 1989; Tan & Lim 1998).

A freshwater species, but according to Last and Compagno (1999), it can be found in estuaries. It is also reported as the most common species in rivers of Thailand (Taniuchi 1998; Wongrat 1998), whereas Tan and Lim (1998) observed more specimens (in the Jambi fish market, Sumatra) during the dry season of July 1997.

Comparisons. — This species is easily distinguished from its congeners i.e. other members of the 'signifer' complex, based on disc shape, morphological characteristics (i.e. colouration, squamation, and skeletal structures), proportional measurements and counts.

Remarks. — Taniuchi (1998) mentioned two forms of *H. signifer* caught from the Chaophraya River, based on the colouration of the dorsal disc surface (i.e. 'white' and 'black'), where he described the former as having 'disc whitish grey with narrow white margin on its outer part, and black on the centre' (figure of a 364 mm DW female specimen shown), and the latter as 'completely black with distinct white margin' (figure of a 270 mm DW male specimen shown).

A juvenile male 139 mm DW (ZRC42993), with fine mid-trunk reticulations as seen in *H. oxyrhyncha*, was determined as a *H. signifer* based on similarities in external and internal characteristics with the latter (i.e. disc shape, more rounded pectoral-fin apex; snout short and snout tip broad; disc with prominent white edge; tail whitish behind sting; and skeletal frame resembling that of a *H. signifer*). This colour pattern is thus considered an aberrant colour form of *H. signifer*.

On the other hand, an image from Fishbase database (Fishbase online, August 2002), indicating a picture of *H. chaophraya* with the caption 'picture Hicha_u1.jpg by Helias, J.-F.', is not that of a *H. chaophraya*, but rather looks to me like a *H. signifer*, or the new unidentified species *H.* sp. G (this study), also from freshwater.

In Sumatra, juvenile specimens of about 200 mm DW are sometimes exported for the ornamental fish trade, while larger individuals are sold as food fish in the local markets (Tan & Lim 1998).

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

USNM 229492[c] (paratype) (Sintang, Kapuas River, Indonesia); ZRC 42547[a,e] (Mekong Basin, Thailand); ZRC 42647[e], ZRC 42648[e] (Batang Hari, Sumatra, Thailand); ZRC 42993, ZRC 42984 (Kapuas Basin, Kalimantan, Indonesia).

Himantura walga (Müller & Henle 1841)

Dwarf whipray

Figures 3.2.5r, 3.2.6a, 3.2.7c, 3.2.8c, 3.2.9j, 3.2.10r, 3.2.11q, 3.2.12l, 5.4.6-5.4.8; Tables 5.4.7-5.4.8

Trygon walga Müller & Henle 1841: 159 (original description based on 10 specimens, location where types are deposited indicated but not catalog numbers, a young female syntype illustrated). Possible syntypes and localities: BMNH 89.2.1.4196, 222 mm disc width, female, Madras (one specimen from BMNH); RMNH – not examined (three specimens from RMNH); MNHN 2337, 198 mm disc width, mature male, Red Sea; MNHN 2431, 170 mm disc width, female, Ganges Delta, India; MNHN 2438, 155 mm disc width, mature male, Pondicherry, India; (six specimens from MNHN, other 3 syntypes not examined) (measurements by P. Last).

Synonymy. —

Trygon heterurus Bleeker 1852: 67 (original description based on a female specimen 165 mm disc width, not figured). Possible holotype: BMNH 1867.11.28.158, 163 mm disc width (measurement by P. Last). Type locality: Batavia (=Java), Indonesia.

Trygon walga: Bleeker 1852, 67 (description). Localities: Batavia (=Java), Samarang (=Semarang), Indonesia.

Trygon (Himantura) walga: Günther 1870, 475 (brief description). Locality: East Indies.

Trygon (Himantura) nuda Günther 1870: 476 (original description based on 4 specimens from India and Singapore). Two possible syntypes: BMNH 1845.3.7.19, 105 mm disc width, immature male; BMNH 1845.3.7.20, 95 mm disc width, immature male (measurements by P. Last). Type locality: Singapore.

Trygon nudus: Martens 1876, 408 (listed). Locality: Singapore.

Leiobatis (Himantura) heterurus: Bleeker 1877, figs. 1a and 1b, pl. 558, Plagiostom. Pl. 36 (illustration of holotype).

Leiobatis (Himantura) walga: Bleeker 1877, figs. 1a and 1b, pl. 563, Plagiostom. Pl. 41 (illustration of male syntype).

Dasybatus (Himanturus) imbricatus: Garman 1913, 379 (description, misidentification in part). Locality: East Indies.

Dasyatis imbricatus: Fowler 1930, 179 (brief description, misidentification in part). Localities: China; Malaysia; Indian Ocean.

Dasybatis uylenburgi Giltay 1933: 13, fig. 3, 4, 5 and 6 (original description based on a male specimen 180 mm disc width, illustrated). Holotype: 27. III. 1929, in the Type Mus. Roy. Hist. nat. Belgique. (But see Walschaerts *in* Eschmeyer [On-line, ver. February 15, 2002], holotype as IRSNB 38). Specimen not examined. Locality: Poeloe Endoe, East Indies.

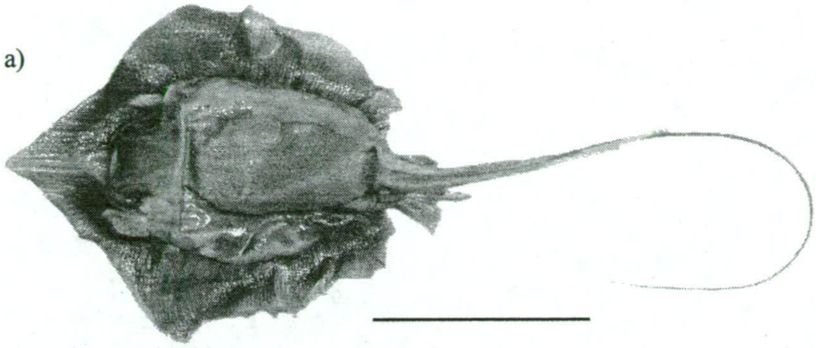
Dasyatis nudus: Fowler 1938, 16 (listed). Locality: Singapore.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc shape oval, centre slightly raised at mid-scapular; preorbital snout moderately long, broadly concave, with a distinct apical lobe; anterior disc margin slightly concave, lateral apices broadly rounded. Dorsal surface of disc uniform light brownish green, with paler disc margins; ventral disc uniform pale (whitish), with darker disc margins; tail uniformly light brownish green on dorsal half from tai base to sting base, pale (yellowish) behing sting to tail tip; ventral half pale whitish. Secondary median denticle band developed along sub-primary denticle band, and independent row of enlarged denticles on tail between tail base and sting base; secondary band broad subrectangular with well-defined margins.

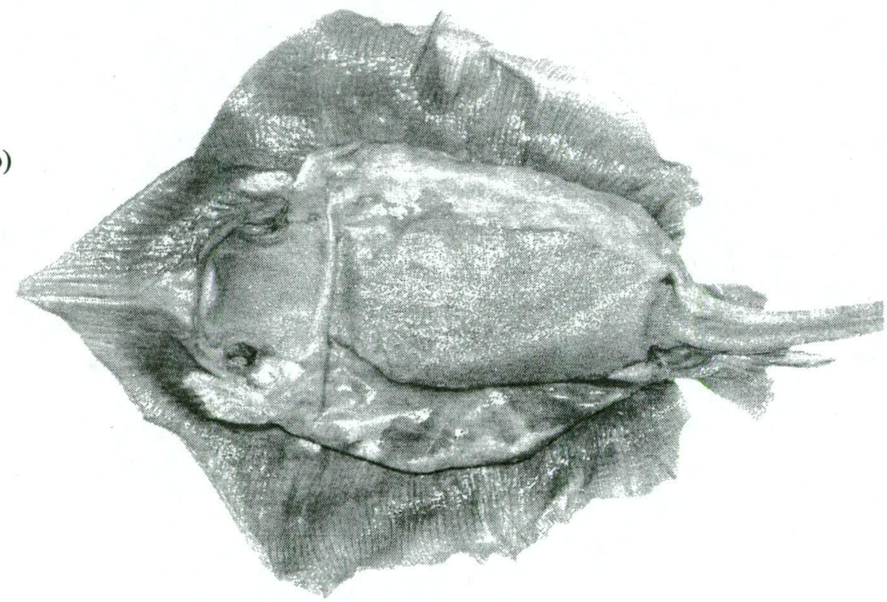
Description. — Disc oval, width 0.90-0.97 in length; flat, center slightly raised at mid-scapular, maximum disc thickness 0.10-0.14 in disc width (DW); preorbital snout moderately long, broadly concave, with a distinct apical lobe, angle 104.5-118^{o}; anterior margins of disc slightly concave, lateral apices broadly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Figs. 5.4.6-5.4.8).

Figure 5.4.6. One of ten possible syntypes of *Himantura walga* in dorsal views. a, whole specimen; b, close-up of disc, indicating denticle band; c, close-up of tail base, indicating enlarged thorns. MNHN 2337 (172 mm DW; mature male; Red Sea). Photos and measurements by P. Last. Bar 10 cm.

a)



b)



c)

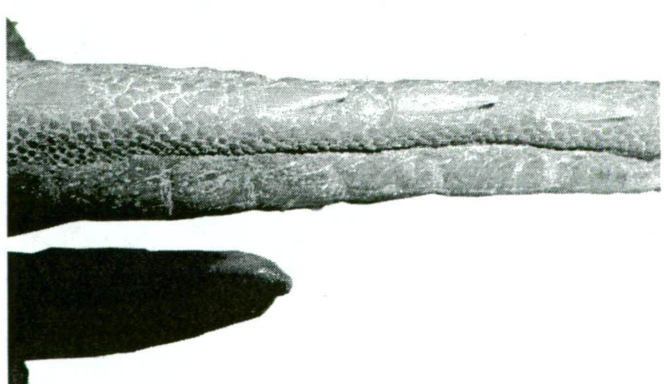


Figure 5.4.7. Illustration of *Himantura walga* (reproduced from Müller & Henle 1841; original copy not seen).

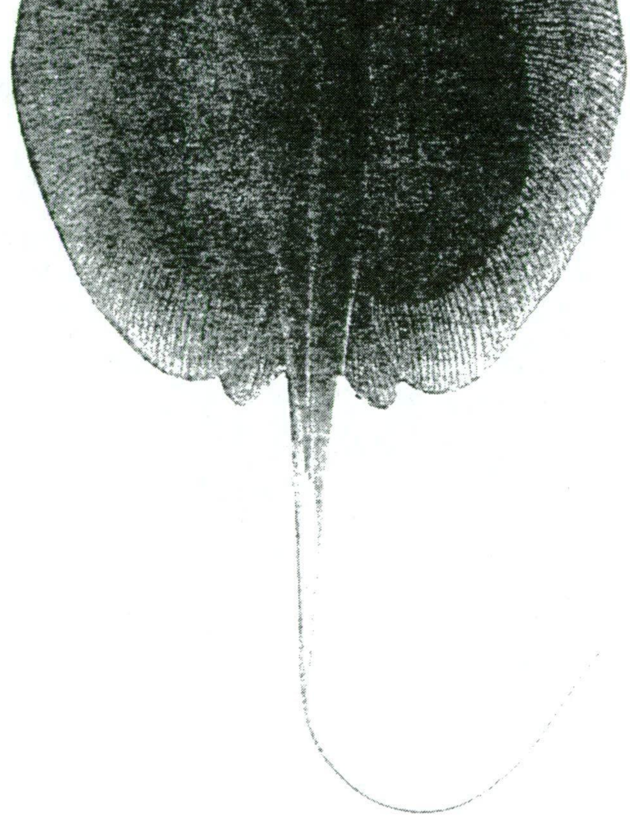
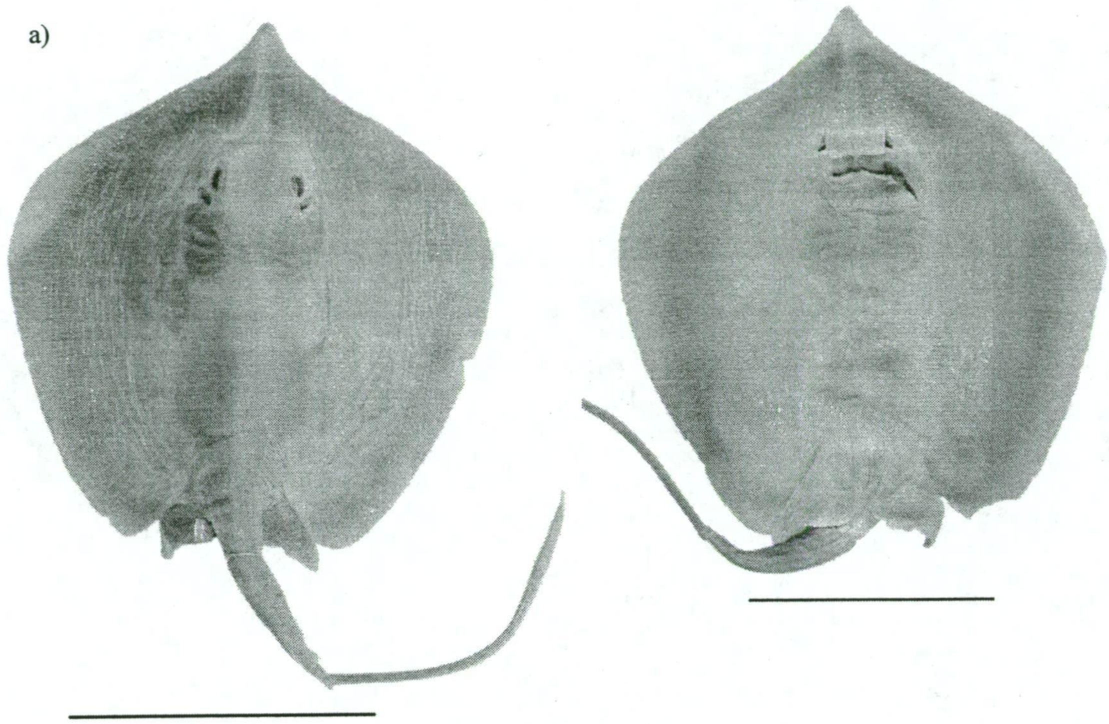
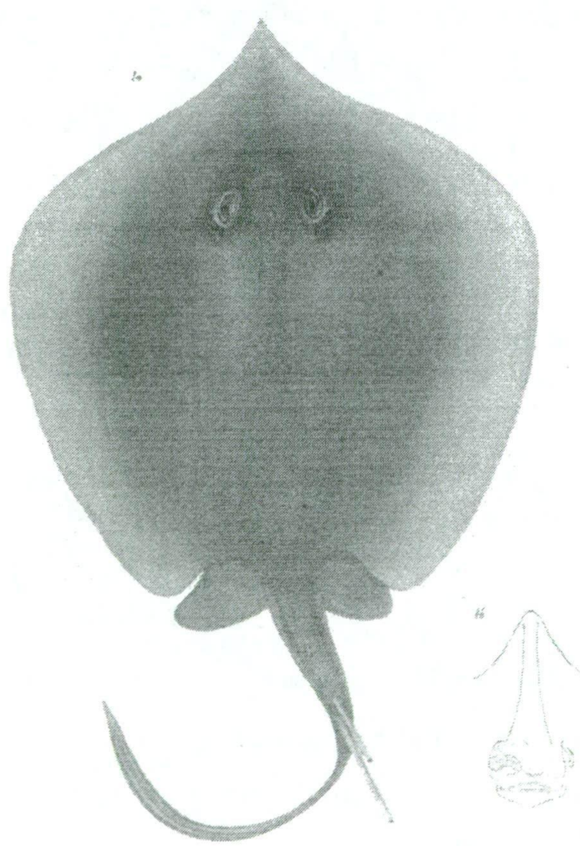


Figure 5.4.8. Holotype of *Trygon heterurus* in dorsal and ventral views. a, BMNH 1867.11.28.158 (163 mm DW; female; Java, Indonesia; photos and measurements by P. Last); b, illustration (reproduced from Bleeker 1877: fig. 1, pl. 558, Plagiostom. Pl. 36). Bars 10 cm.

a)



b)



Pelvic fins long, 18.6-24.5% DW; width across base 12.8-18.7% DW. Claspers of adult male (Fig. 3.2.5r) short and stout, dorsal and ventral surfaces slightly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle long, about 2/3rd of clasper length on its outer margin, weak notch anteriorly. Tail broad-based, whiplike, tapering gently toward sting, length 1.00-1.70 times disc width (slightly longer in males and juveniles, subequal in mature females); base depressed, subcircular in cross-section, width 1.23-2.20 times height at base. Tail constricted at sting base, filamentous beyond sting in mature males, bulbous or club-like with a fine filament distally in mature females (Fig. 5.4.8).

Snout moderately long, depressed; preoral snout length 2.76-4.04 times mouth width, 2.20-3.08 times internarial distance, 27.4-33.2% DW; direct preorbital snout length 2.34-3.01 times interorbital length, horizontal length 2.15-2.87 times interorbital length; snout to maximum disc width 39.7-51.8% DW; interorbital space flat; eye moderately large, diameter 50-90% spiracle length; orbits slightly protruded, diameter 0.83-1.47 in spiracle length, interorbital distance 1.21-2.14 times orbit. Spiracles rectangular-shaped, large, situated dorso-laterally. Nostrils moderately large, laterally expanded, outer margin with a weak concavity, length 0.30-0.48 in internasal distance; internasal distance 0.40-0.58 of prenasal length, 2.10-3.35 times nostril length. Nasal curtain skirt-shaped, relatively broad, width 1.61-2.26 times length; lateral margin weakly concave, smooth edged; posterolateral apex lying within broad groove; posterior margin weakly fringed, and weakly concave.

Mouth moderately arched; shallow oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about half mouth width apart; skin on ventral surface of lower jaw moderately well-corrugated, confined to narrow strip around lips. Mouth floor with 2-3 well-developed papillae; rounded distally, longitudinally flattened; single medial papillae, smaller than outer pair, outer pair almost two times larger than medial papillae; outer pair located at each corner of mouth, widely separated from each other.

Teeth small, subequal in upper and lower jaws; cone-shaped with blunt peak, mature males with pointed (sharp) peak. Tooth rows 40-44 in upper jaw, 50 in lower jaw.

Gill opening margins smooth, straight; length of first gill slit 1.35-1.86 times length of fifth, 0.20-0.41 of mouth width; distance between first gill slits 1.81-2.19 times internasal distance, 0.36-0.44 of ventral head length; distance between fifth gill slits 1.16-1.46 times internasal distance, 0.25-0.30 in ventral head length.

Squamation. — Stages of squamation with narrow overlapping size ranges; with Stages 1-3 including tail denticles simultaneously developing. Secondary denticle band, broad subrectangular with well-defined margins.

Stage 0: from birth (ca. 50 mm DW) — Disc entirely smooth; a small narrow heart-shaped suprascapular denticle (length 1-1.5 mm) appearing during late part of this stage. Dorsal surface of disc of one syntype (MNHN 2438, 155 mm DW), entirely smooth.

Stages 1-3: (ca. 140-170 mm DW) — Development of independent row of enlarged denticles on tail between tail base and sting base, defines the early part of this stage. Secondary denticle scapular patch appearing later (ca. 165 mm DW), seemingly simultaneous with the initial development of the primary, median denticle band above first synarcual.

Primary band developing as a single row of enlarged denticles, consisting of seed-shaped denticles; smaller than suprascapular denticle. Secondary denticle patch closely-set, almost abutted. Enlarged denticles along midline of the tail consisting up to 4 short smooth spinules, subequal in size.

Stage 4: (ca. 155 mm DW) — In early part of this stage, cranial and scapular denticle patches coalesced to form an irregular longitudinal band, constricted at nape; primary denticle band becoming weakly evident.

Late stage four (>160 mm DW) (Fig. 5.4.6), secondary median denticle band well-developed as a broad, continuous subrectangular band with well-defined margins. Band extending to snout in front of orbits, narrowing sharply from front of orbits to a median point on snout; length of naked distal area of snout 50-60% of horizontal preorbital snout length; width confined to interspiracular width, slightly expanded above abdomen before narrowing quite sharply a short distance posteriorly, becoming almost as wide as tail width at pectoral-fin insertion, before extending on to tail adjacent enlarged denticles midline of tail to sting base. Tail beyond sting completely smooth.

Denticles in secondary band largest along median line, decreasing towards lateral margins of band; smaller denticles interspersed among larger ones. Denticles along midline of the tail with 4-6 greatly enlarged spear-shaped thorns, crowns slightly convex, free posterior tip greatly extended from base; progessively larger posteriorly, largest about 3 times length of smallest; uniformly spaced between each other (space equal to length of one of the preceding thorns); posteriormost thorn with bifurcate base.

Stages 5 and 6 not applicable for this species.

Two elongate stinging spines usually present.

Meristics. — Total pectoral-fin radials 98-107 (n=21); propterygium 45-50, mesopterygium 9-15, metapterygium 42-47; pelvic-fin radials 15-26 (n=21); vertebral segments 84-96 (n=20), monospondylous 35-43 (n=20), prespine diplospondylous 38-57 (n=20), and postspine diplospondylous 0-12 (n=19).

Colour. — In fresh, disc uniform light brownish green, with paler disc margins; ventral disc uniform pale (whitish), with darker disc margins. Tail uniformly light brownish green on dorsal half from tai base to sting base, pale (yellowish) behind sting to tail tip; ventral half pale whitish. Lateral surface of tail often with a narrow white line from tail base to tail tip.

Skeletal morphology. — Neurocranium of 200 mm DW mature male (Figs. 3.2.7c, 3.2.8c) with short nasal capsules, anterior edge broadly rounded, slightly convex medially; nasal apertures transversely oval; fontanelle triangular-shaped anteroposteriorly, extending slightly behind level of postorbital process insertion; efferent spiracular artery foramen below optic stalk, just anterior to internal carotid artery foramen on lateral surface of basal plate and midlength of cranium; preorbital processes moderately elongate and robust, posteriorly bluntly pointed; supraorbital crests low and strong, slightly concave along orbital margin sphenopterotic ridge a narrow ledge with straight margins, without lateral process; lateral commissure relatively narrow.

Scapulocoracoid (Fig. 3.2.10r) relatively narrow, high, posterior part moderately extended in lateral view; lateral face subrectangular, with broad base tapering gently upwards and medially to broad articular condyle at tip of scapular process; a relatively large postdorsal foramen; a prominent fenestra on scapular process, connecting anterodorsal fenestra. Lateral face of anterodorsal fenestra sloping gently from inner margin. Procondyle moderately high and long, 2-2.5 times as high as long; mesocondyle short and broad, separated from metacondyle by deep notch; metacondyle about as long as procondyle.

Pelvic girdle (Fig. 3.2.11q) broadly arched, relatively thick, median prepelvic process absent, small anterolateral processes, short dorsal iliac processes, and small mesial ischial processes.

Mixopterygium (Fig. 3.2.12l) relatively simple; 3 basal segments; beta cartilage present as a separate element, merging posteriorly with dorsal marginal cartilage; dorsal marginal cartilage broad, cleaver-shaped, posterior edge not merging with dorsal terminal cartilage, medial flange broad, lateral flange forming the roof of the clasper groove; ventral terminal cartilage large, narrow subtriangular, shaped like an arrowhead; terminal tip of axial cartilage pointed; ventral covering piece, large curved piece of hard cartilage, covering entire lower half of the mixopterygial tip, and narrowly extending to inner lateral surface.

Size. — Birth size around 50 mm DW; length at first maturity (males) between 140 and 150 mm DW. A 139 mm DW male specimen (CSIRO H5471.06) was determined as being an adolescent (maturity stage 3), while a male specimen (MNHN 2438) 159 mm DW, as mature (maturity stage 4). A 184 mm DW female specimen (MTUF 29999) was found gravid with a late term foetus, 48 mm DW.

Etymology. — Not specified.

Common name. — Dwarf whipray (Last & Compagno 1999).

Distribution. — Indonesia (Java; Semarang), Singapore, Malaysia (Sabah; Sarawak) (e.g. Bleeker 1852; Fowler *et al.* 1999). Indian records need further verification, due to confusion with *Himantura imbricata* (Last & Compagno 1999).

Comparisons. — This species is most similar to *H. imbricata* Bloch & Schneider (1801) (see also 'Comparisons' under species heading of *H. imbricata*).

The following comparisons are between representatives of *H. walga* from Borneo (Sabah), and Thailand (Trang, Andaman coast; and Prachnap Khiri Khan, Gulf of Thailand).

The disc shape of young males and females appear slightly more broadly rounded posteriorly compared with adults, or large specimens (in Borneo specimens; Andaman and Thailand Gulf specimens lacking).

Origin of enlarged row(s) of denticle on tail base at about level of pectoral-fin insertion (Borneo), just forward of pectoral-fin insertion (Andaman), and just behind of pectoral-fin insertion (Thailand Gulf). Apparently, the number and size of the denticles are variable among specimens from Borneo, particularly those on the posterior part of the series. In both Andaman and Thailand Gulf specimens, the base of each enlarged denticle is raised, dorsal surface of crown concave, it posterior tip pointed and dorsoposteriorly raised.

The shape of the tip of the tail appears as most variable character among representative specimens from two of three localities (Thailand Gulf specimens lacking), particularly in (relatively) large and/or mature females. However, it is noted that the tail shape of juveniles probably reflects the true tail length/ disc width ratio. The tail tapers to a fine point in both young and mature males, and in young females in all the specimens.

The section behind the sting base of mature females (Borneo specimens) increased in thickness and the tip bulbous (gradation from fine point to club-like shape with filamentous tail tip, observed in maturing females), with weak keels along lateral surface, behind sting tip. As for specimens from Andaman, the tail tip has a short extended filament.

The cross-section of the tail at first sting base, the dorsal surface appear slightly convex and ventral straight to weakly concave (Borneo specimens), dorsal strongly convex in both Andaman and Thailand Gulf specimens, although the ventral surface is moderately notched in Andaman specimens, and ventral strongly notched (deep longitudinal groove present) in Thailand Gulf specimens.

The cross section of the tail at second sting base, the dorsal and ventral surface appear strongly convex (to weakly keeled/ridge in young specimen), and strong lateral keels (Borneo specimens), dorsal and ventral surfaces moderately convex, and weakly notched, with strong lateral ridge (but rather as if two parallel ridges along dorsal and ventral surface tail) (Andaman and Thailand Gulf specimens).

The palate of Borneo specimens is smooth and pigmented; also smooth in Andaman specimens, but granulose in Thailand Gulf specimens.

Remarks. — In the original species description, Müller and Henle (1841) mentioned a total of ten syntypes distributed in a number of museums across Europe. However, they did not provide any catalogue number, but some of which were later listed by Eschmeyer (On-Line, ver. February 15, 2002) (i.e. one BMNH; four MNHN, in addition to MNHN 2337 and MNHN 2431, and three RMNH).

Some of these putative types were examined by P. Last (pers. comm. Dec 2000; June 2001). In addition, Last encountered several possible types in the museums where the syntypes were deposited, and examined these as well.

The number of specimens, including types and possible types of *H. walga*, examined by Last are seven from BMNH, six MNHN, and six RMNH. In the following, putative and possible types are discussed firstly, followed by non-types. It is noted that determining which of these are actually the species was not as straight forward as in *H. imbricata* (see also remarks under that species heading). Nevertheless, based on the results of the present study, it was possible to determine the status of *H. heterurus* (Bleeker 1852), *H. dadong* (Bleeker 1856), and *H. nuda* (Günther 1870).

For the BMNH specimens, only one is supposedly the syntype. Thus, minus the syntypes of three species, i.e. *H. heterurus*, *H. dadong* and *H. nuda*, the number is shortlisted to four. Of the four, one is of unknown locality, while each of the other three came from different localities, which is Muscat (Oman), Penang (Malaysia) and Madras (India). Based on the type locality given in the species description, the possible syntype is most likely the Madras specimen. This specimen BMNH 89.2.1.4196, is a female 222 mm DW, with denticle band well developed.

For the MNHN specimens, two are confirmed as syntypes (MNHN 2337 and MNHN 2431) in agreement with Eschmeyer. MNHN 2337 is a mature male, 198 mm DW from the Red Sea, and MNHN 2431 is a female (maturity stage undetermined), 170 mm DW from Delta Grange (Ganges, India). The other four specimens appear to conform to the characteristics of the description. However, their locality differs from that of the type locality, with one of them unknown, and the rest from 'Gulf of Thailand'.

The specimen with locality unknown is most likely the syntype referred to in the original description, i.e. '*the skin of the youngest one quite smooth*'. This specimen, MNHN 2438, 155 mm DW, mature male, has a patch of denticle band above the fontanelle and a narrow band developing at the tail base to sting origin, but otherwise the dorsal surface is smooth. A smaller specimen, ca. 97.5 mm DW (sex not determined), BMNH 1904.5.25 is completely void of denticles on its dorsal surface. All other specimens including those from BMNH and RMNH have a well-developed denticle band, and none as smooth.

Therefore, this specimen (MNHN 2438) is designated as one of the syntypes. Other unique characteristics of this specimen are the presence of a well-developed stinging spine, the tail not tapering to a point (although it appears as damaged during its lifetime), disc plain yellowish brown, and tail darkish in colour.

As for the three specimens from Gulf of Thailand, these remains as unconfirmed syntype of *H. walga*. It is worth mentioning the denticle band in all three mature males, size between 144-150 mm DW are well-developed as opposed to the designated syntype (MNHN 2438).

For the RMNH specimens, three specimens are listed as the syntypes. Based on type locality, two Batavia/ Singapore specimens are excluded as the possible types. One other specimen is anonymously labeled as *Trygon chindrakee* Cuvier, a name in synonymy thus not available (Eschmeyer). This specimen and the remaining two are all of unknown locality, however, it is likely that all three specimens are the syntypes of *H. walga*.

The description of *H. heterurus* (Bleeker 1852), seem to be based on a single female specimen of *H. walga*, particularly the statement '... *with bulbous tip...*', a sexually dimorphic character overlooked by Bleeker. The examination of the holotype specimen, BMNH 1867.11.28.158, 160 mm DW female, confirmed this argument.

As for *H. nuda* (Günther 1870), one of the two syntypes from 'Indian seas, Singapore' examined, indicates it is the young of *H. walga*, i.e. BMNH 1845.3.7.19, c.93.6 mm DW immature male. No other information were obtained from three other syntypes (also held in BMNH, catalog number as listed by Eschmeyer, are

BMNH 1845.3.7.20, 1851.10.4.101, and 1953.8.10.16) to be able to comment further.

The holotype of *H. uylenburgi* (Giltay 1933) was not examined, but based on the illustration in the original description the disc shape and denticle band mid-trunk resembles a male *H. walga*. Giltay synonymised *H. walga* as *H. imbricata*, when he described this new species.

Materials. — Listing follows specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see Chapter 4), [?]tentative identification pending further study (listed last after respective localities). Type specimens are indicated.

BMNH 89.2.1.4196[c] (possible syntype)(Madras, India); BMNH 1845.3.7.19[c] (paratype of *Trygon nuda*), BMNH 1845.3.7.20[c] (paratype of *Trygon nuda*) (Singapore); BMNH 1867.11.28.158[c] (holotype of *Trygon heterurus*), BMNH 1867.11.28.162[c] (Java, Indonesia); CSIRO H4426.11 (Java, Indonesia); CSIRO H4924.01, CSIRO H4924.02, CSIRO H4924.03, CSIRO H4924.04, CSIRO H4924.05, CSIRO H4924.06, CSIRO H4924.07, CSIRO H4924.08, CSIRO H4924.09, CSIRO H4924.10, CSIRO H4924.11, CSIRO H4924.12, CSIRO H4924.13, CSIRO H4924.14 (Prachnap Khiri Khan, Thailand); CSIRO H4927.04 (Trang, Thailand); CSIRO H5471.04, CSIRO H5471.05, CSIRO H5471.06, CSIRO H5471.07, CSIRO H5474.01[a], CSIRO H5474.02[a], CSIRO H5474.14, CSIRO H5474.15, CSIRO H5474.16, CSIRO H5474.17, CSIRO H5474.18, CSIRO H5474.19, CSIRO H5474.20, CSIRO H5584.07, CSIRO H5584.08, CSIRO H5584.09, UMS MMKK11 (Kota Kinabalu, Sabah, Malaysia); CSIRO H5473.01[e], CSIRO H5473.02[e] (Kudat, Sabah, Malaysia); MNHN 2337[c] (possible syntype)(Red Sea), MNHN 2431[c] (possible syntype)(Ganges Delta, India), MNHN 2438[c] (possible syntype) (Pondicherry, India); MTUF 29998 (Vung Tau, Vietnam); MTUF 29999.

Himantura sp. G

Cooks whipray

Fig. 5.4.9; Tables 5.4.9-5.4.10

Synonymy. —

Himantura bleekeri (non Blyth): Taniuchi 1998, 10, tab. 8, fig. 8 (brief description of two specimens, proportional measurements as percent of disc width of one, which is a male 226 mm disc width, tabulated; mature male figured). Locality: Chao Phraya River, Nakhonsawan Province, Thailand; caught January 1997.

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: freshwater species; disc shape oval, robust, centre raised at mid-scapular; preorbital snout long, weakly concave, distinct apical lobe; anterior disc margin strongly convex, lateral apices evenly rounded. Dorsal surface of disc uniform dark brown, ventrally white to pale pinkish, a small patch on surface of abdomen covered with a few dark brown blotches, prominent dark brown disc margin, including free rear tips of pelvic-fins and posterior tip of claspers; tail dark brown dorsally, ventral half at tail base white, uniformly black beyond sting. Secondary denticle band subrectangular, within which an independent row of enlarged heart- to spear- shape denticles along mid-trunk from above mid-first synarcual to sting base is present.

Description. — Disc oval, width 0.88 in length; robust, centre raised at mid-scapular, maximum disc thickness 0.16 in disc width (DW); preorbital snout long, weakly concave, distinct apical lobe, angle 103.50^{O}; anterior margins of disc strongly convex, lateral apices evenly rounded; posterior margin broadly convex, free rear tip narrowly rounded (Fig. 5.4.9). Pelvic fins broad rectangular, long, 27.2% DW; width across base 15.7% DW. Claspers of the single adult male (MTUF 30001; figure not shown) short and stout, dorsal and ventral surfaces broadly convex, lateral edge convexly arched, and medial edge concave; lining of pseudopera smooth; hypopyle moderately long, about half of clasper length on its outer margin, prominent notch anteriorly. Tail slender and whiplike, tapering gently toward sting, length 2.03 times disc width; base moderately depressed, convex above, flat below, width 1.45 times height at base, subcircular in cross-section at sting base, becoming compressed beyond to tail tip.

Snout long, depressed; preoral snout length 4.74 times mouth width, 3.69 times internarial distance, 31.2% DW; direct preorbital snout length 2.46 times interorbital length, horizontal length 2.41 times interorbital length; snout to maximum disc width 54.0% DW; interorbital space slightly raised; eye moderately large, diameter 52% spiracle length; orbits slightly protruded, diameter 0.71 in spiracle length, interorbital distance 2.62 times orbit. Spiracles subrectangular-shaped, laterally elongated, large, about size of orbits. Nostrils large, laterally expanded, outer margin weakly concave, length 0.61 in internasal distance; internasal distance 0.34 of prenasal length, 1.65 times nostril length. Nasal curtain subrectangular, relatively narrow, width 1.57 times length; lateral margin weakly double concave, smooth edged; posterolateral apex lying within narrow groove of posterior nasal flap; posterior margin weakly fringed, and weakly concave, falling just short of mouth.

Mouth arched, upper jaw double concave; lower jaw strongly convex, midline narrow, slightly flat; weak oronasal groove extending posteriorly from posterolateral edge of mouth to chin, posterior extremity about a quarter mouth width apart; skin on ventral surface of lower jaw feebly corrugated, even around lips. Mouth floor with 2 elongate papillae, rounded distally, longitudinally flattened, subequal in size. Palate with single central longitudinal ridge.

Teeth small, subequal in upper and lower jaws; cone-shaped with pointed (sharp) peak. Tooth rows 24 in upper jaw, 22 in lower jaw.

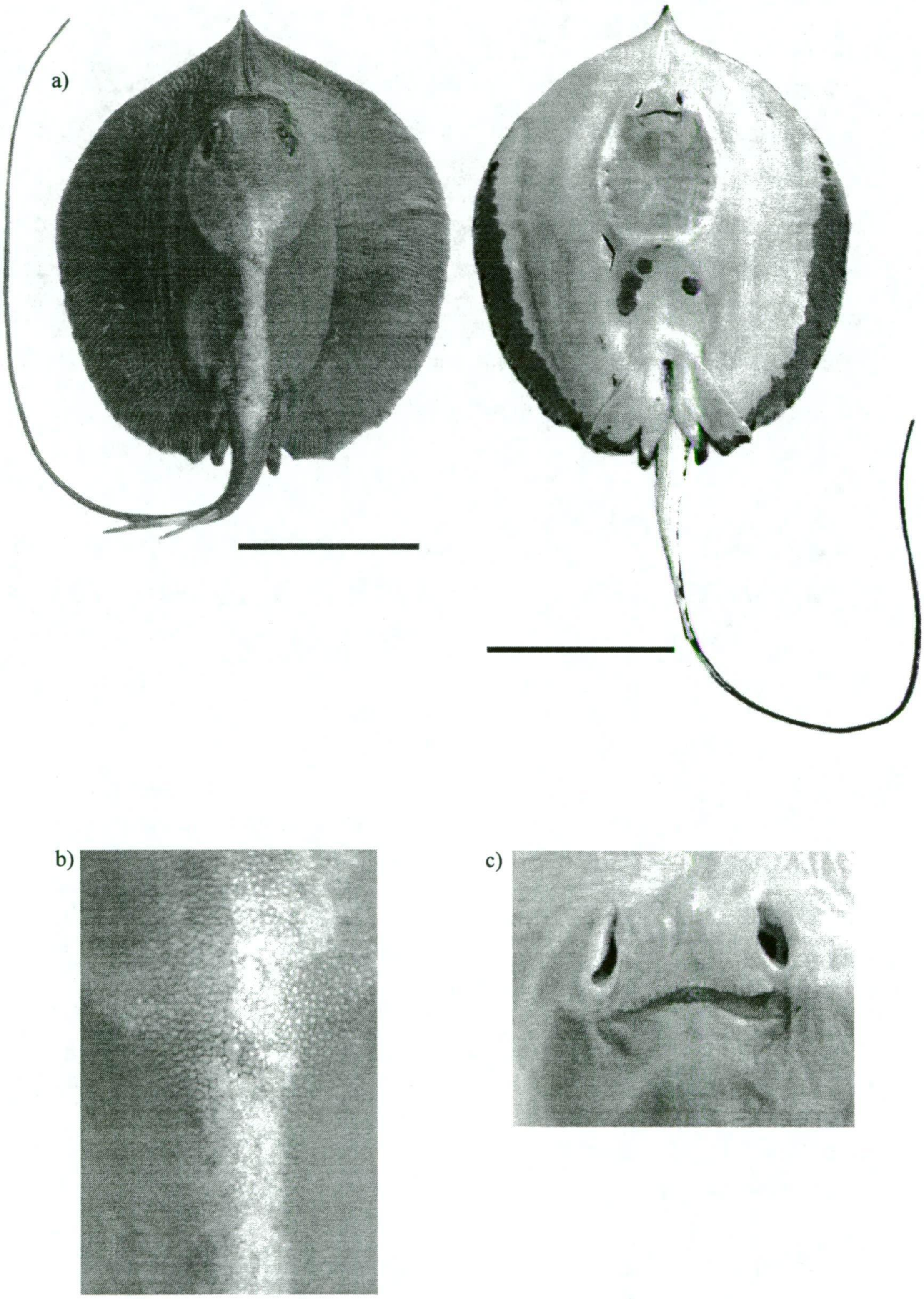
Gill opening margins smooth, straight; length of first gill slit 1.62 times length of fifth, 0.57 of mouth width; distance between first gill slits 2.89 times internasal distance, 0.42 of ventral head length; distance between fifth gill slits 2.17 times internasal distance, 0.31 in ventral head length.

Squamation. — The only specimen in is late part of Stages 3 and 4 (Fig. 5.4.9). Its dorsal surface with a well-developed secondary median denticle band, as a continuous subrectangular longitudinal band with well-defined margin, within which an independent row of enlarged heart- to spear- shape denticles along mid-trunk from above mid-first synarcual to sting base, a single largest (3.1 mm in length) pearl-shaped midscapular denticle present; tail extension well-developed, with well-defined margins. Band extended around (outside) orbits to just anterior of orbits, naked snout ratio 81% in direct preorbital snout length; discontinuous along narrow patch anterolateral of orbits, widening gradually from behind level of orbits, continuing in a more or less straight line along trunk at interspiracular level, before narrowing almost abruptly at level just in front of pectoral-fin insertion, becoming almost horizontally truncated for a distance equivalent to orbit length at pectoral-fin insertion; continuing onto dorsal and dorsolateral surfaces of tail along tail base width, until base of first sting, beyond stings, denticles few and far between; on lateral and ventral surfaces of tail, blunt conical denticles present; anteriorly, band with a slight medial indentation; outside of denticle band, skin smooth, without denticles.

Denticles in band compact, closely-set, small- and large- sized denticles interspersed (not imbricated), the smallest irregularly-shaped denticles occupying spaces between larger (small- and medium- sized) heart-shape denticles; denticles generally small, but appear to be fairly large and abruptly terminating in the band; size largest along the trunk, gradually decreasing towards margins and tail, uniformly small along margin; denticles present on anterior snout margin, although few and far between; interorbital denticles all about the same size as these between the orbit and nuchal area; independent row of enlarged denticles are of irregular sizes (some with their concave to flat base exposed), and uneven distance between them (some closer than that next to it), 4 anterior and 14 posterior of the midscapular denticle.

Two stings present (in single specimen examined); second sting longer, although very similar in shape with first sting, i.e. spear-like, with serrated margins, except at their bases; base of second sting about 15 mm behind base of first sting.

Figure 5.4.9. Representative specimen of *Himantura* sp. G in dorsal and ventral views (a); b, close-up of scapular denticles; c, close-up of oronasal. MTUF 30001 (231 mm DW; mature male; Chao Phraya River, Nakhonsawan, Thailand). Bars 10 cm.


a)
b)
c)

Meristics. — Total pectoral-fin radials 110-111; propterygium 49, mesopterygium 12-13, metapterygium 48-50; pelvic-fin radials 22; vertebral segments 22. Vertebral counts not available from data.

Colour. — In fresh, entire disc uniform dark brown dorsally (elevated area along trunk abraded in the only available specimen), disc plain without any reticulations, a few small black spots scattered randomly on the disc; ventral surface white to pale pinkish, a small patch on surface of abdomen covered with a few dark brown blotches, prominent dark brown disc margin, anterior limit of dark margin at level of first gill slits, extending to posterior disc, including free rear tips of pelvic-fins and posterior tip of claspers. Tail dark brown dorsally, ventral half at tail base white, uniformly black beyond sting. Orbits black above, white below. Upper and lower tooth bands white.

Skeletal morphology. — No dissections were carried out. However, based on x-ray plates, the shape of the neurocranium is of a 'typical' *Himantura*. It is noted, the segmentation of the pectoral-fin radial of the mesopterygial section is unique among other Indo-Pacific *Himantura* in that smaller segments between larger ones are present.

Size. — Neither birth size nor length at first maturity of males and females are known. The single specimen at 231 mm DW is a mature male.

Etymology. — Nil.

Common name. — Cooks whipray, in memory of Sid Cook, Shark Specialist Group Member, Regional Vice Chair for the Northeast Pacific region of the Shark Specialist Group, advisor to the Darwin Project on Elasmobranch Biodiversity, Conservation and Management in Sabah, and friend.

Distribution. — Chao Phraya River, Nakhonsawan Province, Thailand.

Comparisons. — *Himantura* sp. G is easily distinguished from its congeners i.e. other members of the 'signifer' complex based on disc shape, morphological characteristics (i.e. colouration, squamation, and skeletal structures), proportional measurements and counts.

Remarks. — Two specimens of this species identified as *Himantura bleekeri*, were reportedly caught from the Chao Phraya river, Nakhonsawan Province, Thailand, during January 1997 by a team of Japanese and Thai researchers (Taniuchi 1998; H. Ishihara, pers. comm.). In his report, Taniuchi described the specimens as having comparatively long snout (longer than one-third of disc width) with a markedly pointed tip. He remarked the dorsal surface has a striking vase-shaped area with small denticles; the dorsal surface as black in colour, whilst the ventral surface with a black margin. A photograph indicating the dorsal and ventral disc surfaces (Taniuchi, fig. 8) and a table indicating the proportional measurement of one of the specimens (Taniuchi, tab. 8) not examined in this present study, were also included. However, only one of the two, as figured in Taniuchi's report was examined in the present study. Tissue sample obtained from this frozen specimen, unfortunately failed to produce useful DNA sequences (Appendix 4.1.1).

Material. — MTUF 30001 (Thailand).

Himantura marginata (Blyth 1860) *incertae sedis*

Blackedge whipray

Trygon marginatus Blyth 1860: 38 (original description based on several specimens [unspecified number], the largest 1321 mm disc width, no designated types, not figured). Type locality: Calcutta (Lower Bengal), India.

Synonymy. —

Trygon marginatus: Annandale 1909, 30, fig. 5, pl. 3 (fig. 11) (description after Blyth; morphometrics).

Dasybatus (*Himanturus*) *marginatus*: Garman 1913, 378 (description after Blyth).

Amphotistius marginatus: Munro 1955, 14, pl. 3, fig. 40 (description and figure after Annandale). Locality: Ceylon.

Himantura marginata: Compagno & Roberts 1982, 323 (listed).

Diagnosis. — A *Himantura* diagnosed by a combination of the following features: disc oval to subcircular; dorsal surface of disc grey to light albescent-brown; blotched ventrally, with a broad dark disc margin, excluding the anterior disc margin, but including the pelvic-fins, the inner edge of the dark margin consisting of numerous large round spots, some wholly and other partially detached from the rest; tail with similar scattered dark spots on ventral surface at base, which gradually become more numerous and coalescent till they assume a marbled appearance, from mid to tip of tail, entirely dark; this dark colour is more intense in the young, approaching more or less to black, whereas in adults it is weaker and more greyish. Denticles present on entire dorsal and ventral surfaces of the disc, including the tail. Tail without skin fold.

Description. — The following texts are taken directly from Blyth, only rearranged to standardize the presentation, following preceding species descriptions. Texts and comments in parentheses are my own interpretation of his description.

'Disc a trifle (to a small degree) longer than broad, or shorter than broad if the length were measured from front to base of tail. Breadth of one 52 inches (~1321 mm disc width, DW), with tail 83 inches (~2108 mm total length, TL), distance of eyes apart 7 inches (~178 mm); a large fresh specimen 5 feet across (~524 mm DW) with imperfect tail, has just been presented to the (Bengal Asiatic) Society. Anterior margin of the disc exceedingly obtuse, the expanded pectorals being continued forward almost to a transverse line with the medial peak where they unite, on either side of which the outline describes merely a slight concavity. (However, Blyth also noted that) the peak (snout) is stretched out of all shape; the narrow medial peak (apical lobe) of a very large (specimen) just added to the (Medical College) museum projected more than in the young. Tail wholly finless (no skin fold), 1.5 the length of the disc; (usually) one caudal spine (sting) present in every specimen examined, although always have been broken, except for one adult male specimen in the Medical College which has a prefect caudal spine, shown to be 7.15 inches (~182 mm) long.'

Mouth, teeth, and gill opening structures not described.

Squamation. — The squamation was described quite in detail by Blyth; highlighting the presence of denticles on ventral surface of the disc, and tail covered with denticles. However, the developmental stages of squamation (Chapter 2) is not clear from the text, but apparently includes all the stages, except for Stage 3 (development of independent row(s) of enlarged denticles along the midline of the tail).

'In a young female, measuring 18 inches (~457 mm) to base of tail, with greatest breadth of disc 20.5 inches (~521 mm), and tail 29 inches (~737 mm), the tubercles (denticles) generally are less crowded than in the adult, especially on the tail, where there is little indication of their future development.'

'In adults the small limpet-shaped tubercles are disposed not only over the entire upper (dorsal) surface, but also on the broad dark margin of the lower-parts (ventral surface): they are larger and more closely set along the middle, though for the most part not in absolute contact, and are gradually smaller and less crowded laterally, but again become more crowded towards the margin; and there is commonly an irregular range of pointed tubercles larger than the rest on either side, about 3 inches (~76 mm) from the median line in adults. (Additionally), in adults, it is also roughened with minute limpet-shaped tubercles; these appear again about the gill-openings, and more sparingly medially, and a few are scattered over the entire lower surface, which are more readily detected by the feel than by the sight in the fresh specimen.'

'Tail tuberculated all round to within 2.5 inches (~65 mm) of its base underneath, and having scattered and pointed tubercles much larger than the rest above, from its base to the large caudal spine. A larger male specimen in the Medical College, larger than the young female example described earlier, with tail about 40 inches (~1016 mm), and spine 2.75 inches (~70 mm); some small sharp tubercles around the base of the latter (sting). The dorsal tubercles are smaller than in the other; those on the base of the tail more crowded.'

Meristics. — Nil.

Colour. — The colour described by Blyth is presumed to be of fresh specimens, or at least not chemically preserved specimens.

'Grey to light albescent-brown, with a faint blackish wash above (dorsally); buffy-white to more or less of a buffy tinge below (ventrally) with a broad dark border (disc margin) except in front (anteriorly), but including the ventrals (pelvic-fins); this border consisting of numerous large round spots on its inner edge, some wholly and other partially detached from the rest; a few irregular spots are also generally scattered upon the pectorals (disc). The under-surface (ventral) of the tail is white, with similar scattered dark spots, which gradually become more numerous and coalescent till they assume a marbled appearance, and the apical half (from mid to tip of tail) of the tail is wholly dark; this dark colour is more intense in the young, approaching more or less to black; whereas in adults it is weaker and more greyish. From between the eyes to the sides of the tail, and traceable along two-thirds of that organ, are a couple of series of vermiculated lines, (with) a double series of the same along the middle of the back (mid-dorsal).'

Blyth further implied that in the young of both sexes (i.e. males and females), the marginal band of the ventral surface is represented only by a few distantly scattered spots.

Skeletal morphology. — Nil.

Size. — Neither birth size nor length at first maturity of males and females are known. Maximum total length at least 345 cm, and maximum disc width 179 cm, as suggested by Last and Compagno (1999).

Etymology. — According to Blyth, the epithet 'marginatus' is derived from the broad dark margin of the ventral disc surface.

Common name. — Blackedge whipray (Last & Compagno 1999).

Distribution. — Reported in the Bay of Bengal off India, Sri Lanka and Myanmar (e.g. Misra 1947, 1951; Pandey & Sandhu 1992; De Bruin *et al.* 1995). Last and Compagno (1999) suggested this species might venture into Indonesian waters, and possibly off Mozambique.

Comparisons. — See remarks section.

Remarks. — According to Blyth, 'it is by no means a rare species, though seldom to be obtained perfect in the fish-bazaars.' Remarkably however, although also widely reported from the Indian – Bengali region (the type locality is Calcutta on the Lower Bengal), there have been no positive sightings recorded after the original description, except by Annandale (1909), and by Compagno and Roberts (1982). The latter two researchers implied they have seen specimens of this species, when they excluded this species from a list they specifically stated they did not examine.

Others (e.g. Munro 1955; De Bruin *et al.* 1995; Last & Compagno 1999) have used Annandel's illustration (1909: 31, fig. 5) to portray this species.

This species, based on the illustration by Annandale (1909) indicates a rhomboidal disc shape, its lateral apices narrowly angular, and with a particularly unique snout shape. The snout is depicted as being triangular and broad based, but abruptly indented medially, with a small apical lobe present within this medial indentation. However, because Annandale illustrated the species based on a stuffed skin, it cannot be ruled out that what may seem angular might not be so, as the lateral apices might have been too stretched out or distorted during the process of preparing the skin. Furthermore, in his description, Annandale remarked 'though they do not agree in every respect with Blyth's description of the species I think these specimens must belong to it.' This statement, which Annandale did not elaborate upon, and the fact that his illustration was based on a stuffed specimen, suggests that he may have partly misidentified his specimens as that of the mysterious *Himantura marginata.* That the disc is 'longer than wide' (rather than otherwise) as implied by Blyth in his original description, and as pointed out by James (1980), further support the possible error committed by Annandale. James' own observation of *H. marginata* is considered as a misidentification; this is discussed in more detail under the heading of *H. granulata* description.

The mystery of this species is compounded particularly by the widespread presence of denticles on the entire ventral surface of the disc, particularly around the gill openings, and along the disc margin. Additionally, Blyth also mentioned of the presence of an 'irregular range of pointed tubercles larger than the rest on either side (of the dorsal disc surface)' as being 'common'. Such characters have not been observed in any other known *Himantura* species. On the other hand, skates are known to possess several series of enlarged denticles on both sides of the dorsal disc, as well as on both the dorsal and ventral surfaces of the disc (e.g. Deynat & Séret 1996; Deynat 1998).

Blyth's own statement 'I have seen an example of *Trygon marginatus* in the museum of the Calcutta Medical College, which has a central tubercle of moderate size followed by a small one. This, I suspect, is very unusual', also suggests there might be some mix up in the cut up specimens he partly used to describe this species.

Nevertheless, based on Blyth's description of the general disc shape (i.e. ovate), the presence of numerous denticles with stellate base, denticles present on the entire dorsal disc, and general disc (dorsal and ventral) colouration, it appears it might be closely related to *H. chaophraya* (Monkolprasit & Roberts 1990) or *H. granulata* (Macleay 1883). The presence of vermiculated lines along mid-dorsal of the trunk mentioned by Blyth is thought to be the dorsal lateral line, which often is conspicuous in some but not all specimens of other species. Therefore, pending availability of specimens, this species is treated as *incertae sedis*.

Material. — Nil.

CHAPTER 6

6.0 GENERAL DISCUSSION

Overview of the phylogenetic systematics

The phylogeny of the Indo-Pacific *Himantura* which include all known whip-tailed stingrays assigned to this genus following a concurrent taxonomic revision, is presented for the first time. The proposed phylogeny, based on the general taxonomic congruence using separately analysed morphological (Chapter 3) and molecular data sets (mitochondrial DNA sequences of 16S and cytochrome *b*; Chapter 4), demonstrate the genus *Himantura* (excluding amphi-American *Himantura*) as evidently paraphyletic.

First-hand knowledge of the species involved proved particularly important, as despite the resulting phylogenies of both the data sets suggesting a similar pattern of species complexes, bootstrap values were generally low. Furthermore, bootstrap values for deeper relationships were particularly low. Thus, although the evolutionary line among species remains unclear, results from the present study helped clarify the relationships among some of the cryptic species and among distant congeners, i.e. landlocked populations from Thailand, Borneo and Australia.

In analysing the data sets i.e. morphological data set, and molecular data sets generated during this study, the congruence test of Farris *et al.* (1995) was used to assess the distribution, nature, and extent of conflict among data sets instead of just using the test as an automatic justification for the continued separation of character partitions. Such an approach rather reflects the advances in philosophical ideals, particularly regarding analyses of multiple data sets (e.g. Ballard *et al.* 1998; Wiens 1998; Liu & Miyamoto 1999). The low branch support observed in this study is thus attributed to disproportionate ratio of OTU : number of characters in the data matrix (Bremer *et al.* 1999), rather than the OTUs lacking congruency. Moreover, during the same period, and in a relatively short time span since Parker's (1997) review, there has been similar increase in the number of investigations into the phylogeny of other fish groups (e.g. Marcus & McCune 1999; Bargelloni *et al.* 2000; Durand *et al.* 2002).

Based on the present study, members of two other genera in the family, namely *Dasyatis* and *Pastinachus*, are distinguishable from the Indo-Pacific *Himantura* as well as from each other. The genus *Pastinachus* is shown as the most recent common ancestor to the Indo-Pacific *Himantura*, whilst *Pastinachus* spp. form a polytomy with *Dasyatis* spp.

Results of the present analyses lend no support for a closer relationship between members of the Indo-Pacific *Himantura* and members of the genus *Dasyatis*, thus refuting the hypotheses of their close interrelatedness (Nishida 1990; McEachran *et al.* 1996; Rosenberger 2001a). The proposed phylogeny in fact provides additional synapomorphies for the Indo-Pacific whip-tailed stingrays.

Character evolution patterns for the diverse morphological features (disc shape, size at maturity, tail structure, and squamation) as highlighted earlier in the introductory chapter (Chapter 1) is elucidated based on the species subcomplexes defined herein (Chapter 3). It is noted that character distribution among members of the Indo-Pacific *Himantura* is highly homoplastic, although unique (autapomorphic) characteristics are also prevalent. However, when combined with other characters, particularly squamation and clasper characteristics, the tail and tail skin fold characters are found useful in generating a more structured relationship among members of the Indo-Pacific *Himantura* sensu latu. Hence, in combination with having the character tail skin fold lacking or only rudimentary (≤ 1 mm), the Indo-Pacific *Himantura* may be characterized (information on several species were not available at the time of this study) by the presence of a secondary denticle band in sub-adults and adults, denticle shape irregular to rounded with smooth and flat crown, and clasper pseudosiphon positioned on inner margin (of clasper).

The presence of a well-developed secondary denticle band in the Indo-Pacific *Himantura* suggests an advantage in a benthic lifestyle, whereby the anterior-posterior dorsal denticle band functions as a shield, providing additional protection to vital internal organs. This theory is congruent with the terminal positions of these taxa in the phylogeny tree.

With respect to the clasper structure, the absence or presence of a pseudosiphon, and its position when present, suggest a pattern of character evolution in relation to a relatively simplistic structure in derived (stingray) taxa. Species lacking a pseudosiphon apparently possess a pseudorhipidion, which is a small flap positioned between the dorsal margin of the clasper groove and the hypopyle. The pseudosiphon, whose function remains unclear, appears to be a remnant of the deep notch separating the pseudorhipidion from the anterior margin of the hypopyle. When the pseudosiphon is present and located on the anterior of hypopyle near clasper groove, the pseudorhipidion is still present, although appearing less conspicuous. In all of the Indo-Pacific *Himantura* determined as possessing a pseudosiphon that is consistently located on the inner margin of the clasper, the pseudorhipidion is entirely absent. In these taxa, the margins of the clasper groove and hypopyle appear as a simple structure.

Both morphological (this study) and molecular (Sezaki *et al.* 1999) data sets also support the closer relationship between freshwater and marine *Himantura*, and between freshwater and marine *Dasyatis* than between freshwater *Himantura* and freshwater *Dasyatis*, or between marine *Himantura* and marine *Dasyatis*. Furthermore, there is evidence that the genus *Dasyatis* might have a separate Indo-Pacific and Neotropical form, based on initial findings in the present study. Lovejoy (1996) noted a similar trend among the urolophids (genus Urolophus).

The earliest work suggesting a close relationship between dasyatids and urolophids was probably by Chu and Wen (1979). Studying the lateral line canal system of Chinese elasmobranchs, they noted that several members of Chinese urolophids and dasyatids were similar although differing in their tail character (the former having a caudal fin).

Later, Yearsley (1988) noted that the neurocranium of Australian urolophids as most closely resemble that of dasyatid stingrays, and the scapulocoracoid of the Japanese urolophid, *Urolophus aurantiacus*, as most similar to that of the stingray genus *Dasyatis*. Comparison of several skeletal structures (neurocranium, scapulocoracoid and pelvic girdle) between several Indo-Pacific *Dasyatis* spp.

examined in the present study, Yearsley's urolophid specimens and *Taeniura lymma* (see Lovejoy 1996) confirms his (Yearsley's) finding.

Another interesting observation regarding the structure of the pelvic girdle is the presence of a well-developed median prepelvic process in both *Pastinachus* species examined (Fig. 3.2.11b,c), such as that present in the potamotrygonids (South American freshwater stingrays). Current knowledge regarding *Pastinachus* spp. is rather fragmented, with reports of its occurrence in both freshwater and marine habitats across the Indo-Pacific region, and even the taxonomic status of this genus is under review (Chapter 3). It would be interesting to see how these two taxa might be interrelated, as Yearsley (1998) also noted that the similarities in the anatomy of the mixopterygia between Australian urolophids and dasyatid stingrays suggests a closer relationship between these latter two, than with the potamotrygonids.

Taxonomic framework

The whip-tailed stingrays currently described under the genus *Himantura* represent the most speciose batoid fauna in the Southeast Asian subregion. The 21 species recognized herein might be grouped into at least three species complexes based on morphological, biological and physiological evidence. In this study, three complexes are introduced, and tentatively termed 'uarnak', 'uarnacoides', and 'signifer' complexes. Within each complex, sister-pair relationships are shown (Chapter 3). A key to each species complex is formulated, following which each complex is defined. Species descriptions are arranged in alphabetical order under the heading of respective complexes. Thus, to search for the description of a *Himantura* species, a key to the species complex should be consulted firstly.

One of the main discoveries of this study concerns the revelation of cryptic species involving variable colour patterning. New species described in this study include those that were previously misidentified as one of these cryptic species. The type species *Himantura uarnak* is one of the cryptic species, the others being *H. gerrardi, H. toshi, H. undulata* and a previously misidentified species, *H.* sp. A (Chapter 5).

Investigations into squamation characteristics were particularly useful in distinguishing *H. uarnak* from two similarly patterned species, *H. undulata* and *H.* sp. A. In fact, the discovery of squamation characters, which proved to be one of the important diagnostic characters for members of the genus, was initially based on the two sequence data (Chapter 4). The clustering of conspecifics among the cryptic taxa in the resulting phylogenies, led to the detection of ontogenetic development of colour pattern.

The usefulness of squamation characteristics however, is limited when different individuals of putative conspecifics display several colour morphs of similar life stages. In particular are the various colour morphs observed in individuals of *H.* cf. *gerrardi*, *H.* cf. *toshi* and *H.* cf. *uarnak*. Although there is weak evidence to suggest sexual dimorphism, as well as regional colour morphs, additional synapomorphies to reliably identify putative conspecifics are wanting. If however, colour pattern characteristics represent parallelism, as hypothesized by Rosa (1985) for his observations in the potamotrygonids, then more effort should be directed at investigating squamation characters of these (Indo-Pacific *Himantura*) taxa. In such cases, where both morphometric and meristic data are also overlapping, comparison of internal structures including skeletal structures, proved very useful for elucidating additional data.

It is noted that specimens with colour morphs that are considered aberrant due to their rarity has also been observed in the field. Although these are usually observed in large specimens (>500 mm disc width), at least one small specimen (c. 300 mm disc width) have been observed.

The lack of study materials and limited available data (many of the information obtained were based on photographs) is attributed to this unresolved puzzle. A factor remaining as a major challenge in taxonomic studies of stingrays is in dealing with the large size species, which makes them not only difficult to handle, but even hazardous due to their weight and presence of coarse denticles. The inclusion of these various other colour morphs in future molecular studies (particularly when whole intact specimens are lacking) is evidently useful in shedding more light to this puzzle.

Biogeography

Both widespread and restricted species distributional patterns were observed in the Indo-Pacific *Himantura*. Terminal taxa generally have widespread distribution, while basal taxa have disjunct distribution. Among the widespread species, which include species of the uarnak complex, there is evidence indicating regional colour morphs of putative *H. uarnak* conspecifics. However, as mentioned earlier, confirmation of such a pattern is pending availability of additional data. The restricted species on the other hand, refers to coastal and estuarine species with limited geographical distribution, and to freshwater species inhabiting landlocked areas within the region.

The faunal patterns of the coastal and estuarine species is hypothesized as rather a reflection of ecological limitations than patterns of evolution, as suggested by Last and Séret (1999) for much of the Australasian region. For example, the coastal habitats of the South China Sea off Sabah, Brunei, Sarawak and the northern reaches of the Java Sea off Kalimantan of Borneo island are all dominated by the influence of large rivers (TRACC online 2002). However, because the continental shelf is widest (over 100 km) over the Sarawak and southwestern Kalimantan borders, the greater seabed area of muddy environments there results in a markedly different suite of macro-habitats. For this reason, the lineage independence of species within this subregion is likely due to ecological opportunities.

The basal position of landlocked (freshwater) species in the phylogeny of the Indo-Pacific *Himantura* (Chapter 3 and 4) is in favour with Metcalfe's (1998) theory that the East and Southeast Asian continental terranes originated on the margin of India - North and Northwestern Australia of the ancient Gondwanaland. Nevertheless, based on differences in mtDNA and amino acid sequences of complete cytochrome *b* between populations of *H. chaophraya* from India and Thailand, Sezaki *et al.* (1999) implied that allopatric speciation might have taken place. Divergence time estimates from molecular data would have provided stronger support for the hypothesis of the present distribution.

However, in contrary to Last and Séret's (1999) theory regarding ecological replacement of dasyatids and urolophids in northwestern and northeastern Australia, the lower importance of both *Dasyatis* and urolophid taxa from the South China Sea subregion of the Southeast Asian region is hypothesized as an indication of evolutionary pattern. Several of the *Dasyatis* species, including all urolophids are totally absent from the area, although increasing in diversity anti-tropically.

The presence of cryptic taxa and of sister-pair relationships within each species complexes, further suggests a pattern of sympatric (competitive) speciation among stingrays of this group.

Methodological standardization

Methodological standards for the taxonomic description of stingrays are herein introduced. These include proposals for standard usage of terminologies for both external and internal structures. Although designed primarily for whip-tailed stingrays, the proposed methods should be applicable for all other stingray groups. The importance of photographic record or at least an illustration is also emphasized, as descriptive data alone were found to insufficiently reflect what was being described.

Description of the disc shape is based on three main attributes, i.e. the snout, lateral apices and disc margins. These attributes when accounted for separately, offer a better picture of the disc shape being described, especially when good photos of the taxa in question are not available.

For measuring specimens, specimens should be laid in normal resting position whenever possible. Measurements should be taken as direct length (point to point distance), it should be ensured that these are taken from fixed points, as described for the respective measurements. A series of body measurements is introduced, and listed in the order they are taken, so as to minimize specimens handling.

Ambiguities in obtaining meristic data are clarified, particularly regarding pectoral radials distributed across more than one pterygium. The methods for tooth count are specified, and other characters, i.e. oral papillae and rachi, are recommended for counting.

Squamation characters are found as particularly important for both taxonomic and systematics work. For taxonomic purposes, squamation characteristics are described based on its developmental stages. It is noted that the order in which the squamation development is presented, does not mean all species are necessarily in the same order. Denticle band (when present) measurements for quantifying the band shape is particularly useful for systematics work.

CHAPTER 7

7.0 CONCLUSION

This review of the genus *Himantura* is the first since Garman (1913). The overall results of this study illustrate the importance of taxonomic studies for such works as phylogenetic analyses.

Twenty-one species of Indo-Pacific whip-tailed stingray genus *Himantura*, including 7 new species are recognized as a result of the present study. The evolutionary relationship among its members is shown to be paraphyletic, as based on morphological and molecular (mitochondrial DNA) data sets. The genus is herein redefined, using synapomorphies of squamation and clasper characteristics, in combination with the absence of the tail skin fold. However, pending further studies, no change in the generic allocation is proposed.

A major implication of this study is the alpha taxonomy of the Indo-Pacific *Himantura*, following which the status of some of the specimens in designated type series requires revision (Chapter 5). Species descriptions which include proposals for nomenclatural changes, however, is being prepared for publication elsewhere, in partial fulfillment of the requirements by the latest edition of the International Code of Zoological Nomenclature (ICZN 1999).

Comments and suggestions

For taxonomic studies, additional specimens are required for a majority of the species described. Riverine or freshwater species are particularly lacking, but usually it is also the adult specimens of large species that are lacking. With the taxonomy of the Indo-Pacific *Himantura* reasonably good, much effort should now be directed at solving the puzzle among this group of taxa.

For phylogenetic studies, more efforts are required to collect information that is missing in this study. Particular characteristics that need further examination are the branchial arch and musculature. However, the other characters should also be investigated to determine the level of intraspecific variation.

As for molecular phylogenetic studies, this area is advancing at a very fast pace. The latest findings suggest using the mtDNA control region (CR) sequence for elucidating congeneric relationships (Takashi & Goto 2001).

The affinities between *Dasyatis* and Indo-Pacific urolophids, and the hypothesis regarding a separate Indo-Pacific and Neotropical *Dasyatis* also warrants further investigation.

In view of the difficulties experienced in accessing original descriptive papers, I recommend these be made more accessible to the scientific community, if not to the general public. Ideally, these should be made accessible via the internet.

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TABLES

Table 5.2.1. Measurements in % of disc width, for *H. fai* Jordan & Seale 1906. (A) USNM 51712 (holotype, female); (B) CAS 213286(3of3), CAS 213290, CSIRO H2753.01, CSIRO H2754.01, CSIRO H5207.01, CSIRO H5671.01, MTUF 26717 (nontype, males and females). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(A)	(B)			
		Range	N	Mean	S.D.
Disc width (mm)	368.3	320.0 - 985.0	7	601.43	225.96
Total length	n.a	186.9 - 335.0	7	284.24	46.98
Disc length	n.a	84.7 - 89.2	7	86.16	1.59
Snout to pectoral insert	n.a	74.2 - 79.1	7	76.98	1.73
Disc thickness	n.a	9.4 - 13.6	7	11.42	1.82
Snout preorbital	n.a	16.9 - 20.0	7	18.66	1.13
Snout preorbital (horizontal)	n.a	15.0 - 19.1	7	17.44	1.34
Length pelvic-fin	n.a	13.4 - 18.9	7	15.89	1.77
Width across pelvic-fin base	n.a	10.2 - 12.7	7	11.52	0.90
Greatest width across pelvic-fins	n.a	19.5 - 32.2	3	26.18	6.33
Cloaca origin to tail tip	n.a	113.1 - 262.7	7	211.72	47.53
Tail width, axil of pelvics	n.a	5.0 - 6.6	7	5.80	0.54
Tail height, axil of pelvics	n.a	4.3 - 6.0	7	5.25	0.62
Pectoral insertion to sting origin	n.a	32.8 - 38.5	7	35.09	2.07
Cloaca origin to sting	n.a	35.9 - 41.8	7	39.31	2.04
Tail width, base of sting	n.a	1.8 - 2.2	7	1.95	0.14
Tail height, base of sting	n.a	1.9 - 2.7	7	2.36	0.33
Sting length	n.a	9.5 - 17.8	4	13.87	3.60
Snout preoral	n.a	18.0 - 20.1	7	19.19	0.81
Mouth width	n.a	6.8 - 8.4	7	7.29	0.52
Distance between nostrils	n.a	8.3 - 10.3	7	8.96	0.75
Interorbital width	n.a	10.2 - 13.4	5	11.86	1.28
Intereye width	n.a	17.1 - 21.3	5	18.75	1.57
Snout to maximum width	n.a	31.8 - 39.2	7	34.15	3.02
Eye diameter	n.a	2.0 - 4.2	7	2.86	0.70
Orbit diameter	n.a	4.7 - 7.1	7	5.68	0.94
Spiracle length	n.a	4.8 - 7.3	7	5.95	0.78
Interspiracular width	n.a	14.7 - 18.4	5	16.47	1.34
Orbit and spiracle length	n.a	7.3 - 10.4	7	8.71	1.07

...*continued*

Table 5.2.1. continued.

Nostril length	n.a	3.9 - 4.6	7	4.33	0.24
Snout prenasal	n.a	13.5 - 15.5	7	14.67	0.72
Nasal curtain width	n.a	10.0 - 12.4	7	10.82	0.94
Nasal curtain length	n.a	5.1 - 6.2	6	5.40	0.40
End of orbit to pectoral insertion	n.a	52.1 - 58.3	7	54.90	1.86
Snout to origin of cloaca	n.a	68.5 - 76.5	7	72.52	2.53
Width, 1st gill slit	n.a	2.7 - 3.1	7	2.79	0.16
Width, 3rd gill slit	n.a	2.9 - 3.4	7	3.10	0.20
Width, 5th gill slit	n.a	1.6 - 2.2	7	2.03	0.22
Head length	n.a	39.5 - 41.4	7	40.09	0.67
Distance between 1st gill slits	n.a	12.3 - 19.7	7	17.08	2.26
Distance between 5th gill slits	n.a	11.6 - 20.0	7	13.70	3.05
Cloaca length	n.a	0.5 - 4.8	7	3.82	1.48
Clasper, postcloaca length	n.a	6.3 - 7.7	4	7.06	0.62
Clasper, length from pelvic axil	n.a	3.7 - 4.5	4	4.07	0.34

Table 5.2.2. Counts and meristic values for *H. fai*. (*data given in original description).

	(A)	(B)	
		Range	N
Oral papillae (floor)	*4	4 - 4	5
Palate ridges	n.a	3 - 3	4
Upper tooth rows	*13	20 - 22	2
Lower tooth rows	*23	28 - 31	2
Total pectoral radials	154	155 - 157	3
Propterygial radials	61-62	61 - 63	3
Mesopterygial radials	19	18 - 21	3
Metapterygial radials	73-74	72 - 76	3
Total pelvic radials	25-27	23 - 27	3
Total vertebral segments	118	120 - 123	2
Monospondylous vertebrae	51	48 - 52	2
Prespine diplospondylous	67	71 - 102	3
Postspine diplospondylous	0	0 - 0	3

Table 5.2.3a. Measurements in % of disc width, for *H. gerrardi* (Gray 1851). (A) NMV A949 (possible syntype of *T. macrurus*); (B) BMNH 1867.11.28.160 (possible syntype of *T. macrurus*); (C) RMNH 2460, RMNH 2468, RMNH 2469 (possible syntypes of *T. macrurus*). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)	(B)*	(C)*			
			Range	N	Mean	S.D.
Disc width (mm)	252.0	193.7	197.2 - 289.7	3	247.03	46.70
Total length	369.0	419.7	n.a - n.a	3		
Disc length	94.8	95.9	83.2 - 93.4	3	88.22	5.10
Snout to pectoral insert	82.0	86.2	n.a - n.a	3		
Disc thickness	12.5	10.1	n.a - n.a	3		
Snout preorbital	21.5	23.3	19.8 - 21.4	3	20.44	0.82
Snout preorbital (horizontal)	19.2	21.5	n.a - n.a	3		
Length pelvic-fin	17.8	21.2	n.a - n.a	3		
Width across pelvic-fin base	12.1	13.0	n.a - n.a	3		
Greatest width across pelvic-fins	34.1	8.9	n.a - n.a	3		
Cloaca origin to tail tip	n.a	341.2	n.a - n.a	3		
Tail width, axil of pelvics	5.9	4.9	n.a - n.a	3		
Tail height, axil of pelvics	4.7	4.7	n.a - n.a	3		
Pectoral insertion to sting origin	37.4	40.7	n.a - n.a	3		
Cloaca origin to sting	44.1	48.5	n.a - n.a	3		
Tail width, base of sting	1.9	1.6	n.a - n.a	3		
Tail height, base of sting	2.2	2.2	n.a - n.a	3		
Sting length	19.3	x	n.a - n.a	3		
Snout preoral	22.5	23.6	n.a - n.a	3		
Mouth width	6.8	8.4	n.a - n.a	3		
Distance between nostrils	8.4	8.9	n.a - n.a	3		
Interorbital width	11.9	13.5	n.a - n.a	3		
Intereye width	18.4	19.2	n.a - n.a	3		
Snout to maximum width	42.8	45.1	n.a - n.a	3		
Eye diameter	3.6	5.1	n.a - n.a	3		
Orbit diameter	6.1	7.0	n.a - n.a	3		
Spiracle length	7.1	7.5	n.a - n.a	3		
Interspiracular width	17.9	19.2	n.a - n.a	3		
Orbit and spiracle length	10.1	10.9	n.a - n.a	3		

...continued

Table 5.2.3a. continued.

Nostril length	3.8	4.3	n.a - n.a	3
Snout prenasal	16.7	17.9	n.a - n.a	3
Nasal curtain width	8.9	10.4	n.a - n.a	3
Nasal curtain length	5.5	5.2	n.a - n.a	3
End of orbit to pectoral insertion	57.7	59.1	n.a - n.a	3
Snout to origin of cloaca	76.0	78.5	n.a - n.a	3
Width, 1st gill slit	2.2	2.8	n.a - n.a	3
Width, 3rd gill slit	2.6	3.2	n.a - n.a	3
Width, 5th gill slit	1.6	2.1	n.a - n.a	3
Head length	44.2	46.9	n.a - n.a	3
Distance between 1st gill slits	18.2	20.3	n.a - n.a	3
Distance between 5th gill slits	11.4	12.6	n.a - n.a	3
Cloaca length	5.9	5.0	n.a - n.a	3
Clasper, postcloaca length	x	7.6	n.a - n.a	3
Clasper, length from pelvic axil	x	2.5	n.a - n.a	3

Table 5.2.4a. Counts and meristic values for *H. gerrardi*. (*count by P. Last).

	(A)	(B)*	(C)	
			Range	N
Oral papillae (floor)	n.a	4	n.a - n.a	3
Palate ridges	n.a	n.a	n.a - n.a	3
Upper tooth rows	n.a	n.a	n.a - n.a	3
Lower tooth rows	n.a	n.a	n.a - n.a	3
Total pectoral radials	137	n.a	n.a - n.a	3
Propterygial radials	51	n.a	n.a - n.a	3
Mesopterygial radials	22	n.a	n.a - n.a	3
Metapterygial radials	64	n.a	n.a - n.a	3
Total pelvic radials	29-30	n.a	n.a - n.a	3
Total vertebral segments	111	n.a	n.a - n.a	3
Monospondylous vertebrae	44	n.a	n.a - n.a	3
Prespine diplospondylous	67	n.a	n.a - n.a	3
Postspine diplospondylous	0	n.a	0 - 0	3

Table 5.2.3b. Measurements in % of disc width, for *H. gerrardi* (Gray 1851). (D) 'small denticle' variety; (E) 'large denticle' variety. N is number of specimens from which means and standard deviations (S.D.) were taken.

	(D)				(E)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	143.0 - 446.0	43	262.33	62.36	204.0 - 532.0	18	287.72	85.25
Total length	338.7 - 411.7	25	363.28	15.65	346.7 - 417.2	6	378.50	29.87
Disc length	84.3 - 94.3	41	88.28	2.07	86.1 - 94.3	18	90.70	2.47
Snout to pectoral insert	74.5 - 86.2	43	78.88	2.19	77.7 - 84.6	18	80.84	2.14
Disc thickness	9.2 - 14.0	43	11.52	0.97	9.8 - 14.2	18	11.78	1.11
Snout preorbital	18.1 - 22.1	43	19.69	0.78	19.0 - 21.9	18	20.15	0.71
Snout preorbital (horizontal)	16.5 - 20.6	43	18.36	0.93	17.6 - 19.8	18	18.72	0.60
Length pelvic-fin	17.1 - 20.6	41	18.95	0.83	16.3 - 21.6	18	19.83	1.28
Width across pelvic-fin base	9.6 - 13.3	43	11.87	0.81	11.3 - 13.8	18	12.47	0.57
Greatest width across pelvic-fins	22.6 - 38.1	20	28.23	4.73	20.8 - 32.7	6	27.27	4.33
Cloaca origin to tail tip	268.5 - 336.4	25	289.24	14.46	272.7 - 339.1	6	304.45	27.96
Tail width, axil of pelvics	5.0 - 7.2	43	5.89	0.47	5.0 - 7.8	18	6.55	0.77
Tail height, axil of pelvics	3.7 - 5.5	43	4.51	0.38	3.6 - 8.9	18	4.59	1.16
Pectoral insertion to sting origin	25.0 - 38.7	43	31.99	3.09	28.7 - 38.1	11	33.30	3.42
Cloaca origin to sting	32.2 - 44.4	43	36.95	2.97	33.7 - 43.7	11	38.52	3.54
Tail width, base of sting	1.4 - 2.4	41	2.01	0.22	1.9 - 2.5	11	2.14	0.19
Tail height, base of sting	1.7 - 2.6	41	2.10	0.19	1.9 - 2.5	11	2.16	0.20
Sting length	x - x	43			x - x	18		
Snout preoral	19.4 - 23.2	43	21.20	0.79	20.5 - 22.8	18	21.63	0.64
Mouth width	6.2 - 7.9	43	6.94	0.36	0.0 - 7.7	18	6.22	2.30
Distance between nostrils	7.1 - 9.4	43	8.27	0.50	7.7 - 9.2	18	8.41	0.44
Interorbital width	8.9 - 13.4	43	11.43	0.85	10.6 - 13.1	18	11.93	0.71
Intereye width	14.9 - 23.2	43	17.79	1.47	16.6 - 20.1	18	18.38	1.04
Snout to maximum width	33.4 - 42.4	42	38.55	2.21	35.1 - 43.2	18	39.09	2.02
Eye diameter	3.0 - 6.0	43	4.33	0.59	2.6 - 5.6	18	4.48	0.76
Orbit diameter	5.0 - 8.4	43	6.69	0.80	4.5 - 8.7	18	6.78	1.02
Spiracle length	5.7 - 9.8	43	6.58	0.67	4.8 - 7.7	18	6.46	0.74
Interspiracular width	14.5 - 20.7	43	17.14	1.18	16.3 - 19.4	18	17.74	0.84
Orbit and spiracle length	8.7 - 17.5	43	10.12	1.31	8.7 - 11.6	18	10.26	0.80

Table 5.2.3b. continued.

Nostril length	3.3 - 5.0	43	4.32	0.32	3.8 - 4.6	18	4.33	0.21
Snout prenasal	14.3 - 17.2	43	15.85	0.65	15.4 - 17.1	18	16.30	0.44
Nasal curtain width	8.6 - 11.5	43	9.82	0.59	9.4 - 11.2	18	10.29	0.47
Nasal curtain length	4.6 - 6.7	43	5.52	0.44	4.9 - 6.2	18	5.50	0.34
End of orbit to pectoral insertion	50.4 - 61.4	43	54.82	1.94	53.3 - 60.0	18	56.32	1.78
Snout to origin of cloaca	69.4 - 81.8	43	73.22	2.45	71.4 - 78.1	18	74.40	1.95
Width, 1st gill slit	1.9 - 3.1	43	2.57	0.25	2.3 - 3.0	18	2.73	0.21
Width, 3rd gill slit	2.4 - 3.4	43	2.83	0.24	2.5 - 3.4	18	2.95	0.23
Width, 5th gill slit	1.4 - 2.2	43	1.79	0.19	1.5 - 3.0	18	1.96	0.31
Head length	38.8 - 45.2	43	41.46	1.42	40.4 - 44.6	18	42.49	1.23
Distance between 1st gill slits	15.6 - 20.4	43	17.18	1.03	16.8 - 19.5	18	18.04	0.95
Distance between 5th gill slits	9.3 - 13.0	43	10.61	0.68	10.1 - 11.9	18	10.94	0.51
Cloaca length	3.2 - 6.2	43	4.60	0.65	4.5 - 6.7	18	5.20	0.60
Clasper, postcloaca length	7.7 - 17.1	26	8.94	1.81	7.6 - 18.0	13	9.35	2.72
Clasper, length from pelvic axil	4.2 - 12.5	26	5.31	1.56	4.5 - 14.5	13	5.60	2.68

Table 5.2.4b. Counts and meristic values for *H. gerrardi*.

	(D)		(E)	
	Range	N	Range	N
Oral papillae (floor)	2 - 5	12	2 - 4	9
Palate ridges	3 - 3	18	3 - 3	8
Upper tooth rows	22 - 22	1	24 - 26	2
Lower tooth rows	25 - 27	1	29 - 30	2
Total pectoral radials	129 - 138	34	131 - 140	15
Propterygial radials	49 - 52	34	49 - 53	15
Mesopterygial radials	20 - 24	34	19 - 23	15
Metapterygial radials	58 - 67	34	62 - 67	15
Total pelvic radials	22 - 30	34	23 - 31	15
Total vertebral segments	106 - 115	34	106 - 118	9
Monospondylous vertebrae	43 - 53	34	41 - 56	15
Prespine diplospondylous	56 - 72	34	58 - 73	9
Postspine diplospondylous	0 - 0	34	0 - 0	5

Table 5.2.5. Measurements in % of disc width, for *H. jenkinsii* (Annandale 1909). (A) 'jenkinsii' variety; (B) RUSI 996 (holotype of *H. draco*); (C) 'draco' variety. N is number of specimens from which means and standard deviations (S.D.) were taken. (*data given in original description).

	(A)				(B)*	(C)			
	Range	N	Mean	S.D.		Range	N	Mean	S.D.
Disc width (mm)	231.0 - 912.0	11	375.36	212.70	561.0	273.0 - 711.0	4	531.50	195.49
Total length	180.4 - 220.9	6	208.64	15.67	n.a	193.8 - 204.3	4	199.32	4.89
Disc length	87.4 - 94.9	11	91.98	2.65	n.a	88.3 - 94.5	4	90.80	2.79
Snout to pectoral insert	77.9 - 84.8	10	82.14	2.38	n.a	78.5 - 82.9	4	80.55	1.91
Disc thickness	9.6 - 12.9	10	11.61	1.04	11.2	9.9 - 13.1	4	11.47	1.30
Snout preorbital	20.0 - 23.9	11	22.19	1.13	n.a	21.6 - 22.4	4	21.97	0.36
Snout preorbital (horizontal)	19.2 - 22.7	11	21.00	1.07	n.a	20.7 - 21.6	4	21.23	0.45
Length pelvic-fin	16.0 - 18.9	10	17.96	1.02	15.9	17.2 - 18.5	4	17.98	0.65
Width across pelvic-fin base	10.1 - 11.8	11	11.07	0.52	n.a	9.0 - 11.6	4	10.75	1.16
Greatest width across pelvic-fins	18.1 - 32.1	9	26.52	4.84	n.a	21.3 - 25.0	3	23.11	1.88
Cloaca origin to tail tip	106.8 - 139.0	5	128.68	14.06	n.a	116.0 - 130.3	4	125.01	6.56
Tail width, axil of pelvics	5.8 - 8.3	11	7.00	0.82	n.a	6.3 - 6.8	4	6.59	0.18
Tail height, axil of pelvics	4.8 - 6.3	10	5.59	0.49	n.a	4.9 - 5.0	4	4.97	0.07
Pectoral insertion to sting origin	30.9 - 42.5	7	37.92	4.02	n.a	30.1 - 31.5	4	30.72	0.55
Cloaca origin to sting	6.2 - 45.2	7	37.00	13.74	n.a	35.8 - 37.0	4	36.41	0.56
Tail width, base of sting	2.1 - 3.3	7	2.92	0.42	n.a	2.3 - 3.0	4	2.69	0.31
Tail height, base of sting	2.3 - 3.5	7	3.01	0.42	n.a	2.7 - 3.1	4	2.88	0.19
Sting 1 length	13.8 - 16.2	4	14.58	1.12	n.a	13.1 - 13.1	1	13.12	
Sting 2 length	x - x	4			2.0?	19.9 - 21.0	2	20.47	0.74
Snout preoral	20.2 - 24.4	11	22.82	1.13	20.7	21.5 - 24.1	4	22.43	1.15
Mouth width	6.3 - 7.8	10	6.99	0.49	n.a	6.2 - 7.3	4	6.76	0.46
Distance between nostrils	9.1 - 11.3	11	10.06	0.69	n.a	8.9 - 10.7	4	9.70	0.80
Interorbital width	9.9 - 15.9	11	12.04	1.96	n.a	9.7 - 11.2	4	10.42	0.66
Intereye width	16.0 - 25.4	11	20.84	3.34	n.a	15.5 - 20.0	4	17.13	2.08
Snout to maximum width	31.4 - 37.9	10	35.58	2.21	n.a	32.7 - 39.4	4	35.69	2.80
Eye diameter	2.7 - 6.2	11	4.85	1.13	n.a	2.9 - 4.7	4	3.59	0.79
Orbit diameter	4.6 - 8.0	11	6.79	1.22	n.a	4.3 - 7.8	4	5.76	1.56
Spiracle length	5.3 - 8.2	11	6.70	0.90	n.a	5.5 - 6.3	4	5.98	0.41
Interspiracular width	14.8 - 20.5	11	17.80	2.18	n.a	14.3 - 18.3	4	15.65	1.85
Orbit and spiracle length	7.8 - 11.8	11	10.21	1.31	n.a	7.4 - 10.9	4	8.95	1.51

...continued

Table 5.2.5. continued.

Nostril length	3.1 - 4.7	11	4.02	0.51	n.a	3.9 - 4.7	4	4.12	0.37
Snout prenasal	15.6 - 19.1	11	17.86	0.95	n.a	16.4 - 18.9	4	17.45	1.03
Nasal curtain width	10.3 - 12.1	11	11.04	0.56	n.a	10.0 - 11.5	4	10.78	0.60
Nasal curtain length	5.3 - 6.2	11	5.74	0.37	n.a	5.4 - 5.9	4	5.65	0.24
End of orbit to pectoral insertion	52.7 - 57.2	11	54.83	1.52	n.a	52.8 - 55.2	4	54.34	1.08
Snout to origin of cloaca	73.2 - 82.6	10	77.88	3.26	n.a	72.4 - 77.8	4	74.31	2.39
Width, 1st gill slit	2.5 - 3.2	11	2.92	0.21	n.a	2.8 - 3.1	4	2.96	0.10
Width, 3rd gill slit	2.9 - 3.6	11	3.24	0.20	n.a	3.1 - 3.3	4	3.19	0.06
Width, 5th gill slit	1.9 - 2.3	11	2.13	0.13	n.a	1.8 - 2.2	4	2.03	0.19
Head length	40.8 - 47.3	10	45.18	2.01	n.a	41.4 - 46.7	4	43.59	2.26
Distance between 1st gill slits	16.7 - 19.7	11	18.41	1.02	n.a	17.4 - 20.2	4	18.20	1.33
Distance between 5th gill slits	10.2 - 12.3	11	11.39	0.66	n.a	10.5 - 12.1	4	11.10	0.76
Cloaca length	3.3 - 5.6	11	4.29	0.56	n.a	3.6 - 4.7	4	4.13	0.56
Clasper, postcloaca length	7.9 - 17.3	5	10.63	3.85	n.a	12.3 - 12.3	1	12.31	
Clasper, length from pelvic axil	4.7 - 12.2	5	6.82	3.09	n.a	8.4 - 8.4	1	8.41	

Table 5.2.6. Counts and meristic values for *H. jenkinsii.* (*data given in original description).

	(A)		(B)*	(C)	
	Range	N		Range	N
Oral papillae (floor)	2 - 4	5	2	n.a - n.a	4
Palate ridges	3 - 3	5	n.a	n.a - n.a	4
Upper tooth rows	n.a - n.a	5	28	n.a - n.a	4
Lower tooth rows	n.a - n.a	5	31	n.a - n.a	4
Total pectoral radials	145 - 151	4	148	147 - 148	2
Propterygial radials	56 - 60	4	n.a	57 - 60	2
Mesopterygial radials	19 - 23	4	n.a	19 - 20	2
Metapterygial radials	66 - 71	4	n.a	68 - 71	2
Total pelvic radials	24 - 28	4	22	27 - 30	2
Total vertebral segments	117 - 118	2	158	123 - 125	2
Monospondylous vertebrae	45 - 48	4	11	49 - 49	1
Prespine diplospondylous	70 - 72	3	68	74 - 74	1
Postspine diplospondylous	0 - 0	2	0	0 - 0	1

Table 5.2.7a. Measurements in % of disc width, for *H. toshi* Whitley 1939. (A) AMS IA39 (holotype, male); (B) QM I12946 (nontype, female, Moreton Bay, Queensland); (C) CSIRO CA1245, CSIRO CA3994, CSIRO H1034.1, CSIRO H1464.4, CSIRO H4077.01, CSIRO H4077.02, CSIRO H4077.03, CSIRO H4077.04 (nontype, males and females, North West Shelf, Western Australia). N is number of specimens from which means and standard deviations (S.D.) were taken. (*distorted, not in natural position).

	(A)	(B)	(C)			
			Range	N	Mean	S.D.
Disc width (mm)	294.0	247.0	205.0 - 312.0	8	226.27	35.32
Total length	306.5	320.6	293.3 - 364.7	8	345.83	22.55
Disc length	89.2	92.3	84.0 - 89.9	8	88.23	2.06
Snout to pectoral insert	80.4	81.8	76.2 - 81.0	8	79.44	1.60
Disc thickness	11.2	11.6	10.9 - 12.6	8	11.54	0.55
Snout preorbital	21.5	21.3	17.9 - 21.1	8	20.27	1.07
Snout preorbital (horizontal)	20.0	20.3	17.4 - 19.6	8	18.77	0.77
Length pelvic-fin	16.5	19.0	17.2 - 18.8	8	18.03	0.60
Width across pelvic-fin base	10.5	11.8	8.8 - 12.1	8	10.95	1.03
Greatest width across pelvic-fins	*28.2	25.4	20.8 - 25.4	5	23.10	1.67
Cloaca origin to tail tip	229.9	242.7	222.8 - 291.4	8	270.96	21.00
Tail width, axil of pelvics	5.6	6.0	5.0 - 6.7	8	5.89	0.51
Tail height, axil of pelvics	4.6	4.9	4.4 - 6.8	8	5.16	0.83
Pectoral insertion to sting origin	35.5	33.3	30.8 - 38.8	8	35.96	2.35
Cloaca origin to sting	39.0	38.5	32.3 - 44.2	8	39.25	3.36
Tail width, base of sting	1.7	2.1	1.4 - 2.4	8	2.11	0.31
Tail height, base of sting	2.1	2.3	2.0 - 2.6	8	2.36	0.19
Sting 1 length	14.5	n.a	9.7 - 14.6	7	12.84	1.59
Sting 2 length	x	x	x - x	7		
Snout preoral	22.8	23.6	20.8 - 22.4	8	21.56	0.57
Mouth width	6.5	6.4	6.7 - 8.2	8	7.44	0.42
Distance between nostrils	9.9	9.8	9.0 - 9.6	8	9.40	0.22
Interorbital width	11.3	12.4	10.2 - 14.4	8	12.28	1.51
Intereye width	17.4	20.0	16.5 - 22.3	8	20.72	1.78
Snout to maximum width	37.4	41.9	33.2 - 42.5	8	39.57	3.58
Eye diameter	4.0	4.4	3.1 - 4.6	8	4.21	0.52
Orbit diameter	7.2	6.5	5.9 - 7.0	8	6.35	0.38
Spiracle length	5.2	5.4	5.7 - 8.6	8	7.63	0.87
Interspiracular width	16.9	18.2	15.1 - 19.4	8	18.04	1.39
Orbit and spiracle length	9.6	9.7	9.5 - 11.6	8	10.43	0.79

...continued

Table 5.2.7a. continued.

Nostril length	5.2	4.6	4.4 - 4.9	8	4.70	0.16
Snout prenasal	17.0	17.8	15.7 - 16.9	8	16.29	0.49
Nasal curtain width	10.6	10.9	10.2 - 10.9	8	10.54	0.28
Nasal curtain length	6.6	6.6	6.0 - 6.6	8	6.37	0.22
End of orbit to pectoral insertion	53.7	55.4	52.6 - 57.2	8	55.11	1.70
Snout to origin of cloaca	76.5	77.9	70.5 - 76.8	8	74.87	2.21
Width, 1st gill slit	2.9	2.7	2.3 - 2.7	8	2.48	0.18
Width, 3rd gill slit	2.8	2.9	2.4 - 3.0	8	2.72	0.18
Width, 5th gill slit	1.7	1.6	1.4 - 2.0	8	1.70	0.20
Head length	43.2	44.4	40.0 - 43.1	8	41.97	1.07
Distance between 1st gill slits	17.2	17.8	15.4 - 21.0	8	17.38	2.01
Distance between 5th gill slits	10.7	10.9	9.5 - 13.0	8	10.84	1.28
Cloaca length	4.3	5.1	3.4 - 4.6	8	4.02	0.42
Clasper, postcloaca length	7.4	x	8.4 - 9.0	5	8.72	0.28
Clasper, length from pelvic axil	6.0	x	4.9 - 6.1	5	5.44	0.59

Table 5.2.8a. Counts and meristic values for *H. toshi*.

	(A)	(B)	(C)	
			Range	N
Oral papillae (floor)	4	4	4 - 4	8
Palate ridges	3	3	3 - 3	8
Upper tooth rows	n.a	n.a	21 - 29	8
Lower tooth rows	n.a	n.a	21 - 33	8
Total pectoral radials	132-134	133-134	129 - 136	4
Propterygial radials	51	51-52	48 - 50	4
Mesopterygial radials	16-18	17	19 - 24	4
Metapterygial radials	63-67	65	58 - 64	4
Total pelvic radials	24	27-28	20 - 26	4
Total vertebral segments	98	105	95 - 102	4
Monospondylous vertebrae	n.a	48	46 - 52	2
Prespine diplospondylous	n.a	56	47 - 56	2
Postspine diplospondylous	0	0	0 - 0	2

Table 5.2.7b. Measurements in % of disc width, for *H. toshi* Whitley 1939. (D) CSIRO CA2406, CSIRO CA4271, CSIRO H635.1, CSIRO H635.03, CSIRO H635.04(2of2), CSIRO H963.1, CSIRO H963.3, CSIRO T698, CSIRO T700, CSIRO H3373.02, CSIRO H3373.03, CSIRO H3373.08, CSIRO H3373.09, CSIRO H3380.02, CSIRO H3381.02, CSIRO H3381.03 (nontype, males and females, <300 mm DW); (E) CSIRO H312.1, CSIRO H959.1, CSIRO H959.2, CSIRO H959.4, CSIRO H964.1, CSIRO H964.2, CSIRO H1220.01, CSIRO H1222.1, CSIRO H3329.01, CSIRO H3352.01, CSIRO H3369.01, CSIRO H3387.03, CSIRO H5588.01, CSIRO H5589.01, CSIRO T699 (nontype, males and females, >300 mm DW). Locality: Arafura Sea - Gulf of Carpentaria. N is number of specimens from which means and standard deviations (S.D.) were taken.

	(D)				(E)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	143.0 - 263.0	16	189.70	34.53	334.0 - 592.0	15	446.67	87.23
Total length	326.4 - 416.1	15	359.87	24.04	212.5 - 314.4	10	288.93	30.46
Disc length	85.7 - 100.0	17	90.42	3.91	80.7 - 89.2	15	84.54	2.01
Snout to pectoral insert	76.4 - 88.5	17	81.12	2.99	73.0 - 80.5	15	75.51	1.93
Disc thickness	9.6 - 13.2	17	11.57	1.08	8.3 - 11.8	15	9.66	0.99
Snout preorbital	18.6 - 23.4	17	20.37	1.29	17.1 - 20.6	15	19.03	0.91
Snout preorbital (horizontal)	17.0 - 20.7	17	18.67	1.03	16.6 - 19.0	15	17.88	0.72
Length pelvic-fin	16.7 - 19.6	17	18.19	0.80	16.1 - 19.4	15	17.65	0.89
Width across pelvic-fin base	9.5 - 12.6	17	11.33	0.66	5.9 - 11.2	15	9.58	1.14
Greatest width across pelvic-fins	22.1 - 25.3	7	23.93	1.27	20.2 - 30.4	9	25.23	3.22
Cloaca origin to tail tip	255.1 - 330.2	15	282.65	20.59	141.7 - 245.2	10	218.98	30.45
Tail width, axil of pelvics	4.9 - 7.9	16	6.25	0.62	4.1 - 5.9	15	5.09	0.49
Tail height, axil of pelvics	4.2 - 6.1	16	5.14	0.58	1.3 - 4.7	15	3.96	0.79
Pectoral insertion to sting origin	32.3 - 44.1	16	37.03	3.39	28.4 - 35.0	15	32.68	2.10
Cloaca origin to sting	37.2 - 46.2	16	40.73	2.66	32.2 - 40.7	15	37.62	2.45
Tail width, base of sting	1.6 - 2.9	16	2.24	0.33	1.2 - 1.8	15	1.56	0.16
Tail height, base of sting	2.0 - 2.9	16	2.53	0.39	1.6 - 2.3	15	1.99	0.19
Sting 1 length	9.2 - 16.2	15	12.65	2.11	10.4 - 12.7	2	11.56	1.60
Sting 2 length	x - x	15			7.9 - 16.2	2	12.05	5.83
Snout preoral	20.7 - 25.4	16	22.33	1.32	18.4 - 23.2	15	20.04	1.13
Mouth width	6.7 - 8.8	16	7.75	0.69	6.1 - 7.1	15	6.57	0.32
Distance between nostrils	9.5 - 11.0	16	9.98	0.40	8.2 - 10.3	15	8.75	0.51
Interorbital width	10.7 - 14.2	16	12.22	1.25	9.7 - 11.6	15	10.69	0.51
Intereye width	17.4 - 27.3	16	21.91	2.99	14.6 - 16.5	15	15.51	0.44
Snout to maximum width	37.4 - 46.5	16	41.73	2.41	36.2 - 43.1	15	39.25	1.77
Eye diameter	3.5 - 5.1	16	4.35	0.50	2.3 - 3.5	15	2.97	0.36
Orbit diameter	6.4 - 7.7	16	7.03	0.49	4.0 - 6.2	15	5.20	0.65
Spiracle length	5.8 - 10.2	16	8.27	1.57	4.7 - 5.7	15	5.15	0.26
Interspiracular width	16.6 - 23.1	16	19.54	2.04	13.9 - 16.1	15	14.89	0.64
Orbit and spiracle length	9.6 - 14.0	16	11.82	1.45	7.1 - 9.4	15	8.28	0.56

...continued

Table 5.2.7b. continued.

Nostril length	4.2 - 5.6	16	4.83	0.40	3.8 - 5.1	15	4.21	0.32
Snout prenasal	15.6 - 18.6	16	16.79	0.80	14.1 - 16.2	15	15.24	0.58
Nasal curtain width	10.2 - 12.4	16	10.93	0.55	9.4 - 10.4	12	9.90	0.32
Nasal curtain length	6.2 - 7.6	16	6.72	0.38	5.4 - 7.4	15	6.02	0.50
End of orbit to pectoral insertion	52.1 - 63.8	16	57.27	2.84	50.2 - 57.1	15	52.99	1.92
Snout to origin of cloaca	71.3 - 85.9	16	76.97	3.80	67.7 - 75.0	15	69.86	1.79
Width, 1st gill slit	2.1 - 3.2	16	2.75	0.27	2.4 - 2.9	15	2.63	0.14
Width, 3rd gill slit	2.4 - 3.6	16	2.95	0.31	2.7 - 3.2	15	2.90	0.15
Width, 5th gill slit	1.5 - 2.9	16	1.93	0.36	1.6 - 2.0	15	1.79	0.11
Head length	40.6 - 50.0	16	43.86	2.60	37.8 - 41.7	15	39.07	1.02
Distance between 1st gill slits	15.7 - 18.9	16	17.14	0.91	14.6 - 17.4	15	15.73	0.70
Distance between 5th gill slits	9.7 - 12.0	16	10.43	0.67	8.9 - 11.1	15	9.47	0.59
Cloaca length	3.4 - 5.2	16	4.10	0.55	3.7 - 5.2	15	4.45	0.47
Clasper, postcloaca length	8.9 - 11.4	8	9.82	0.79	8.5 - 17.9	7	14.20	3.53
Clasper, length from pelvic axil	5.0 - 7.0	8	5.98	0.62	4.8 - 14.4	7	10.22	3.69

Table 5.2.8b. Counts and meristic values for *H. toshi.*

	(D)		(E)	
	Range	N	Range	N
Oral papillae (floor)	4 - 4	13	4 - 4	6
Palate ridges	3 - 3	13	3 - 3	6
Upper tooth rows	21 - 29	13	21 - 29	6
Lower tooth rows	21 - 33	13	21 - 33	6
Total pectoral radials	n.a - n.a	5	132 - 135	5
Propterygial radials	n.a - n.a	5	48 - 50	5
Mesopterygial radials	n.a - n.a	5	20 - 23	5
Metapterygial radials	n.a - n.a	5	61 - 65	5
Total pelvic radials	n.a - n.a	5	23 - 29	5
Total vertebral segments	96 - 100	5	94 - 103	5
Monospondylous vertebrae	n.a - n.a	5	44 - 51	5
Prespine diplospondylous	n.a - n.a	5	48 - 54	5
Postspine diplospondylous	0 - 0	5	0 - 0	5

Table 5.2.7c. Measurements in % of disc width, for *H. toshi* Whitley 1939. (F) CSIRO H2376.01, CSIRO H2376.02, CSIRO H2376.03 (nontype, males, off Cairns); (G) CSIRO H38.1, CSIRO H4913.02, CSIRO H4914.01 (nontype, males and a female, Irian Jaya - New Guinea). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(F)				(G)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	231.0 - 383.0	3	289.00	82.15	245.0 - 363.0	3	289.33	64.24
Total length	344.2 - 344.2	1	344.16		351.0 - 355.4	2	353.20	3.09
Disc length	87.6 - 88.2	3	87.82	0.32	86.9 - 100.3	3	92.74	6.84
Snout to pectoral insert	78.4 - 88.6	3	82.14	5.57	74.7 - 80.9	3	77.73	3.09
Disc thickness	8.7 - 11.5	3	10.49	1.59	8.3 - 11.0	3	9.89	1.44
Snout preorbital	18.5 - 20.6	3	19.80	1.10	18.7 - 20.5	3	19.72	0.93
Snout preorbital (horizontal)	16.5 - 19.3	3	17.78	1.42	17.8 - 19.5	3	18.80	0.88
Length pelvic-fin	17.9 - 19.5	3	18.43	0.89	18.1 - 19.0	3	18.52	0.44
Width across pelvic-fin base	10.2 - 10.7	3	10.41	0.25	9.0 - 11.2	3	10.23	1.10
Greatest width across pelvic-fins	25.3 - 30.1	2	27.66	3.39	n.a - n.a	3		
Cloaca origin to tail tip	268.6 - 268.6	1	268.57		274.9 - 284.1	2	279.51	6.51
Tail width, axil of pelvics	5.1 - 6.9	3	5.90	0.89	4.8 - 5.9	3	5.41	0.52
Tail height, axil of pelvics	4.3 - 5.4	3	4.72	0.55	4.1 - 4.6	3	4.44	0.26
Pectoral insertion to sting origin	34.5 - 35.2	3	34.83	0.36	32.0 - 37.5	3	34.11	2.93
Cloaca origin to sting	35.2 - 40.6	3	37.90	2.68	35.7 - 41.1	3	38.32	2.71
Tail width, base of sting	1.8 - 2.0	3	1.87	0.11	1.6 - 1.9	3	1.79	0.17
Tail height, base of sting	2.1 - 2.3	3	2.25	0.12	2.0 - 2.1	3	2.08	0.03
Sting 1 length	13.5 - 19.2	3	15.53	3.23	12.8 - 15.8	2	14.31	2.12
Sting 2 length	19.1 - 19.1	1	19.11		x - x	2		
Snout preoral	21.3 - 22.6	3	21.96	0.67	20.9 - 21.8	3	21.29	0.47
Mouth width	6.6 - 7.3	3	7.04	0.34	6.4 - 6.8	3	6.57	0.19
Distance between nostrils	9.6 - 9.7	3	9.68	0.04	9.1 - 10.0	3	9.45	0.50
Interorbital width	10.7 - 11.6	3	11.22	0.50	10.4 - 17.2	3	12.93	3.69
Intereye width	18.1 - 19.2	3	18.52	0.58	11.3 - 18.2	3	15.01	3.47
Snout to maximum width	40.6 - 43.2	3	41.91	1.29	39.4 - 44.0	3	41.89	2.34
Eye diameter	3.7 - 5.7	3	4.54	1.02	3.4 - 4.3	3	3.91	0.46
Orbit diameter	6.1 - 7.2	3	6.76	0.61	5.4 - 7.3	3	6.63	1.07
Spiracle length	5.7 - 6.1	3	5.96	0.19	5.0 - 5.6	3	5.28	0.30
Interspiracular width	16.8 - 18.4	3	17.41	0.86	15.4 - 17.7	3	16.31	1.23
Orbit and spiracle length	10.2 - 10.4	3	10.33	0.12	8.6 - 10.6	3	9.65	1.01

...continued

Table 5.2.7c. continued.

Nostril length	3.1 - 5.1	3	4.26	1.01	4.0 - 5.0	3	4.63	0.58
Snout prenasal	16.6 - 17.6	3	17.25	0.54	15.7 - 17.3	3	16.34	0.82
Nasal curtain width	10.6 - 10.9	3	10.73	0.19	9.8 - 11.0	3	10.33	0.59
Nasal curtain length	6.5 - 6.6	3	6.55	0.06	5.8 - 6.6	3	6.28	0.44
End of orbit to pectoral insertion	54.5 - 56.5	3	55.65	1.05	51.6 - 56.4	3	53.62	2.47
Snout to origin of cloaca	72.6 - 75.6	3	74.01	1.51	70.5 - 76.1	3	72.62	3.05
Width, 1st gill slit	2.4 - 3.2	3	2.75	0.43	2.3 - 2.9	3	2.67	0.28
Width, 3rd gill slit	2.7 - 3.1	3	2.87	0.16	2.7 - 3.1	3	2.90	0.18
Width, 5th gill slit	1.6 - 2.5	3	2.09	0.47	1.3 - 1.7	3	1.52	0.21
Head length	41.5 - 42.6	3	42.17	0.57	39.7 - 43.4	3	41.39	1.86
Distance between 1st gill slits	16.7 - 17.3	3	17.05	0.30	15.7 - 17.2	3	16.38	0.75
Distance between 5th gill slits	10.4 - 10.4	3	10.39	0.03	9.2 - 11.0	3	10.11	0.89
Cloaca length	3.8 - 5.1	3	4.29	0.70	3.4 - 4.5	3	4.09	0.64
Clasper, postcloaca length	9.1 - 9.7	3	9.34	0.32	8.7 - 9.6	2	9.19	0.64
Clasper, length from pelvic axil	4.6 - 5.6	3	5.18	0.55	5.4 - 5.7	2	5.52	0.19

Table 5.2.8c. Counts and meristic values for *H. toshi*.

	(F)		(G)	
	Range	N	Range	N
Oral papillae (floor)	4 - 4	3	4 - 4	3
Palate ridges	3 - 3	3	3 - 3	3
Upper tooth rows	21 - 29	3	21 - 29	3
Lower tooth rows	21 - 33	3	21 - 33	3
Total pectoral radials	133 - 135	1	132 - 135	3
Propterygial radials	48 - 48	1	49 - 50	3
Mesopterygial radials	24 - 24	1	20 - 21	3
Metapterygial radials	61 - 63	1	63 - 65	3
Total pelvic radials	24 - 24	1	23 - 28	3
Total vertebral segments	102 - 102	1	99 - 102	3
Monospondylous vertebrae	49 - 49	1	42 - 46	3
Prespine diplospondylous	53 - 53	1	53 - 57	3
Postspine diplospondylous	0 - 0	1	0 - 0	3

Table 5.2.9a. Measurements in % of disc width, for *H. uarnak* (Forsskål 1775). (A) BMNH 1953.8.10.15 (holotype of *T. punctatus*); (B) CAS 213281 (nontype, female, Thailand); (C) CSIRO H4130.01, SUML BRU115, SUML BRU112 (nontype, males and a female, Philippines). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)	(C)			
			Range	N	Mean	S.D.
Disc width (mm)	276.0	320.0	271.0 - 363.0	3	311.00	47.16
Total length	413.4	354.4	n.a - n.a	3		
Disc length	97.2	93.8	90.6 - 97.0	3	93.94	3.21
Snout to pectoral insert	85.7	n.a	80.1 - 86.2	3	82.94	3.06
Disc thickness	11.2	11.3	10.6 - 11.3	3	11.00	0.37
Snout preorbital	20.8	21.4	20.1 - 22.4	3	21.16	1.16
Snout preorbital (horizontal)	19.0	20.0	17.2 - 19.2	3	18.39	1.09
Length pelvic-fin	20.3	20.2	18.8 - 19.6	3	19.31	0.42
Width across pelvic-fin base	13.7	12.5	12.3 - 13.8	3	13.13	0.78
Greatest width across pelvic-fins	10.9	30.5	30.5 - 38.7	2	34.59	5.77
Cloaca origin to tail tip	331.5	277.0	n.a - n.a	3		
Tail width, axil of pelvics	6.6	7.5	6.4 - 7.7	3	7.02	0.68
Tail height, axil of pelvics	4.5	5.0	5.0 - 5.0	2	5.02	0.03
Pectoral insertion to sting origin	45.8	39.5	n.a - n.a	3		
Cloaca origin to sting	55.5	43.1	n.a - n.a	3		
Tail width, base of sting	2.0	2.4	n.a - n.a	3		
Tail height, base of sting	2.3	2.4	n.a - n.a	3		
Sting 1 length	n.a	n.a	n.a - n.a	3		
Sting 2 length	x	x	n.a - n.a	3		
Snout preoral	23.1	21.5	19.2 - 21.6	3	20.79	1.35
Mouth width	7.7	7.0	7.6 - 8.2	3	7.96	0.33
Distance between nostrils	8.7	7.8	7.6 - 8.3	3	7.89	0.39
Interorbital width	13.6	13.1	12.4 - 13.7	3	13.16	0.65
Intereye width	20.7	22.4	19.1 - 23.1	3	20.95	1.97
Snout to maximum width	38.0	36.7	38.1 - 42.0	3	39.74	1.98
Eye diameter	4.6	3.5	3.6 - 4.5	3	4.10	0.44
Orbit diameter	6.5	5.8	3.7 - 6.2	3	4.91	1.24
Spiracle length	6.5	6.0	7.5 - 7.6	3	7.51	0.07
Interspiracular width	20.5	19.5	17.1 - 20.8	3	18.99	1.86
Orbit and spiracle length	9.9	9.0	8.8 - 10.0	3	9.30	0.64

...continued

Table 5.2.9a. continued.

Nostril length	4.5	4.4	4.1 - 5.0	3	4.64	0.46
Snout prenasal	17.6	15.8	15.0 - 16.6	3	15.99	0.83
Nasal curtain width	9.9	10.2	10.5 - 11.0	3	10.73	0.23
Nasal curtain length	5.1	5.5	4.7 - 5.7	3	5.30	0.56
End of orbit to pectoral insertion	59.4	n.a	53.6 - 60.8	3	56.91	3.64
Snout to origin of cloaca	81.9	77.4	73.2 - 81.2	3	77.72	4.08
Width, 1st gill slit	2.7	2.7	2.6 - 3.1	3	2.86	0.24
Width, 3rd gill slit	2.9	2.8	3.0 - 3.4	3	3.17	0.24
Width, 5th gill slit	2.2	2.0	1.8 - 2.1	3	1.95	0.11
Head length	47.2	43.4	42.0 - 45.6	3	44.00	1.82
Distance between 1st gill slits	20.2	19.4	19.4 - 52.5	3	30.53	19.01
Distance between 5th gill slits	13.6	12.4	11.6 - 12.3	3	11.93	0.31
Cloaca length	6.4	3.4	3.6 - 5.2	3	4.41	0.81
Clasper, postcloaca length	x	x	8.9 - 9.5	2	9.20	0.46
Clasper, length from pelvic axil	x	x	5.0 - 5.8	2	5.40	0.58

Table 5.2.10a. Counts and meristic values for *H. uarnak*. (*counts by P. Last).

	(A)*	(B)	(C)	
			Range	N
Oral papillae (floor)	5	n.a	n.a - n.a	3
Palate ridges	3	n.a	n.a - n.a	3
Upper tooth rows	n.a	n.a	n.a - n.a	3
Lower tooth rows	n.a	n.a	n.a - n.a	3
Total pectoral radials	n.a	154	n.a - n.a	3
Propterygial radials	n.a	62	n.a - n.a	3
Mesopterygial radials	n.a	20-23	n.a - n.a	3
Metapterygial radials	n.a	69-72	n.a - n.a	3
Total pelvic radials	n.a	32-33	n.a - n.a	3
Total vertebral segments	n.a	126	n.a - n.a	3
Monospondylous vertebrae	n.a	55	n.a - n.a	3
Prespine diplospondylous	n.a	71	n.a - n.a	3
Postspine diplospondylous	n.a	0	n.a - n.a	3

Table 5.2.9b. Measurements in % of disc width, for *H. uarnak* (Forsskål 1775). (D) CSIRO H5477.01, CSIRO H5477.02, CSIRO H5482.01, CSIRO H5484.01, CSIRO H5617.01 (nontype, males and a female, Sabah, Malaysia); (E) CSIRO H5476.03 and three unregistered specimens (nontype, males and a female, Sabah, Malaysia). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(D)				(E)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	264.0 - 373.0	5	298.80	44.87	845.0 - 940.0	4	902.50	40.52
Total length	365.7 - 365.7	1	365.70		91.5 - 91.5	1	91.49	
Disc length	93.9 - 99.2	5	95.50	2.23	85.8 - 91.5	4	88.42	2.35
Snout to pectoral insert	81.9 - 87.4	5	84.75	2.11	78.2 - 78.2	1	78.24	
Disc thickness	10.5 - 13.4	4	12.11	1.29	11.5 - 11.5	1	11.49	
Snout preorbital	20.4 - 23.3	5	21.46	1.11	20.0 - 20.9	2	20.47	0.67
Snout preorbital (horizontal)	18.2 - 21.7	5	19.34	1.42	18.7 - 19.4	2	19.09	0.51
Length pelvic-fin	18.1 - 21.6	5	20.55	1.41	21.5 - 21.5	1	21.51	
Width across pelvic-fin base	12.3 - 13.3	5	12.84	0.51	12.0 - 13.1	3	12.37	0.61
Greatest width across pelvic-fins	23.1 - 36.8	5	30.14	5.82	26.8 - 26.8	1	26.78	
Cloaca origin to tail tip	288.7 - 288.7	1	288.67		n.a - n.a	4		
Tail width, axil of pelvics	6.9 - 9.7	5	8.35	1.06	5.4 - 6.0	4	5.79	0.29
Tail height, axil of pelvics	5.0 - 7.5	5	5.96	1.00	3.4 - 4.7	4	3.93	0.55
Pectoral insertion to sting origin	39.6 - 39.6	1	39.58		36.1 - 36.1	1	36.09	
Cloaca origin to sting	44.8 - 44.8	1	44.79		n.a - n.a	4		
Tail width, base of sting	2.0 - 2.6	2	2.30	0.37	1.9 - 1.9	1	1.89	
Tail height, base of sting	2.1 - 2.5	2	2.29	0.22	1.8 - 1.8	1	1.83	
Sting 1 length	n.a - n.a	5			n.a - n.a	4		
Sting 2 length	x - x	5			x - x	4		
Snout preoral	20.6 - 24.6	5	21.80	1.64	18.7 - 19.3	3	19.03	0.31
Mouth width	6.4 - 8.0	5	7.08	0.67	5.9 - 6.7	4	6.27	0.35
Distance between nostrils	7.8 - 9.0	5	8.34	0.47	7.3 - 7.8	4	7.50	0.21
Interorbital width	12.7 - 15.3	5	14.27	1.05	12.7 - 13.5	4	13.10	0.33
Intereye width	20.4 - 24.1	5	21.97	1.43	16.9 - 18.2	4	17.53	0.54
Snout to maximum width	34.7 - 41.5	5	36.85	2.94	n.a - n.a	4		
Eye diameter	3.8 - 5.0	5	4.40	0.47	1.7 - 2.4	4	2.00	0.29
Orbit diameter	5.3 - 6.7	5	6.03	0.54	3.2 - 4.1	4	3.64	0.43
Spiracle length	6.7 - 9.1	5	7.86	1.04	5.8 - 6.0	4	5.88	0.09
Interspiracular width	19.5 - 20.8	5	20.05	0.58	13.9 - 16.2	4	15.28	0.97
Orbit and spiracle length	9.4 - 11.2	5	10.47	0.72	7.2 - 8.0	4	7.62	0.36

...continued

Table 5.2.9b. continued.

Nostril length	4.6 - 5.0	5	4.79	0.15	3.7 - 4.3	4	3.94	0.32
Snout prenasal	15.2 - 18.1	5	16.20	1.13	14.1 - 14.6	3	14.38	0.29
Nasal curtain width	10.3 - 12.3	5	10.88	0.81	9.4 - 10.6	4	9.88	0.49
Nasal curtain length	5.4 - 5.9	5	5.65	0.20	4.8 - 5.7	4	5.38	0.39
End of orbit to pectoral insertion	57.9 - 63.1	5	60.81	2.11	54.6 - 56.0	2	55.34	0.99
Snout to origin of cloaca	77.0 - 81.6	5	79.68	1.98	69.9 - 69.9	1	69.95	
Width, 1st gill slit	2.6 - 3.2	5	2.82	0.25	2.7 - 3.2	3	3.02	0.28
Width, 3rd gill slit	3.0 - 3.4	5	3.13	0.20	3.0 - 3.5	3	3.26	0.29
Width, 5th gill slit	2.0 - 2.2	5	2.09	0.06	2.0 - 2.5	3	2.25	0.26
Head length	43.0 - 47.9	5	44.72	1.97	39.3 - 40.1	3	39.70	0.39
Distance between 1st gill slits	18.4 - 21.6	5	19.91	1.13	17.5 - 17.8	2	17.66	0.20
Distance between 5th gill slits	11.4 - 15.0	5	12.77	1.34	11.0 - 11.7	2	11.37	0.52
Cloaca length	3.7 - 6.0	5	4.50	1.00	4.5 - 6.2	4	5.35	0.75
Clasper, postcloaca length	8.8 - 10.2	4	9.56	0.60	12.2 - 18.6	3	16.37	3.60
Clasper, length from pelvic axil	4.7 - 5.2	4	4.89	0.25	7.4 - 13.2	3	10.81	3.05

Table 5.2.10b. Counts and meristic values for *H. uarnak*.

	(D)		(E)	
	Range	N	Range	N
Oral papillae (floor)	5 - 5	2	4 - 4	1
Palate ridges	3 - 3	2	3 - 3	1
Upper tooth rows	n.a - n.a	5	n.a - n.a	1
Lower tooth rows	n.a - n.a	5	n.a - n.a	1
Total pectoral radials	146 - 154	5	n.a - n.a	4
Propterygial radials	57 - 64	5	n.a - n.a	4
Mesopterygial radials	18 - 22	5	n.a - n.a	4
Metapterygial radials	66 - 70	5	n.a - n.a	4
Total pelvic radials	25 - 32	5	n.a - n.a	4
Total vertebral segments	n.a - n.a	5	n.a - n.a	4
Monospondylous vertebrae	50 - 53	4	n.a - n.a	4
Prespine diplospondylous	n.a - n.a	4	n.a - n.a	4
Postspine diplospondylous	0 - 0	5	n.a - n.a	4

Table 5.2.9c. Measurements in % of disc width, for *H. uarnak* (Forsskål 1775). (F) CSIRO H1134.1, CSIRO H1134.2, CSIRO H1463.3, CSIRO H2371.02, CSIRO H2371.03, CSIRO H2371.04, CSIRO H2371.05 (nontype, males and females, Western Australia); (G) CSIRO H4016.01, CSIRO H4422.01, CSIRO H4542.06, CSIRO H4786.02, NTM S.11144.001, NTM S.11507.006 (nontype, males and a female, Northen Territory). N is number of specimens from which means and standard deviations (S.D.) were taken. (*tail tip damaged in several specimens).

	(F)				(G)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	275.0 - 295.0	7	286.86	6.89	284.0 - 353.0	6	317.83	22.32
Total length	380.3 - 425.9	7	403.36	17.69	175.9 - 429.9	6	332.21	92.29
Disc length	93.6 - 100.0	7	96.24	2.11	92.5 - 97.5	6	95.43	1.80
Snout to pectoral insert	83.5 - 90.2	7	85.92	2.20	83.1 - 86.2	6	85.11	1.24
Disc thickness	11.7 - 13.8	7	12.61	0.72	9.8 - 12.5	6	11.24	0.91
Snout preorbital	20.4 - 24.1	7	21.51	1.32	20.4 - 22.4	6	21.41	0.81
Snout preorbital (horizontal)	16.9 - 21.0	7	19.38	1.32	18.5 - 21.3	6	19.86	1.18
Length pelvic-fin	19.6 - 20.5	6	20.07	0.31	20.3 - 23.6	6	21.37	1.16
Width across pelvic-fin base	12.4 - 14.4	7	13.30	0.65	11.4 - 13.4	6	12.54	0.79
Greatest width across pelvic-fins	26.6 - 34.7	7	29.43	2.77	18.7 - 31.9	6	27.54	4.97
Cloaca origin to tail tip	298.9 - 343.6	7	320.55	17.15	*98.3 - 348.0	6	252.47	90.53
Tail width, axil of pelvics	7.7 - 8.3	7	7.90	0.20	4.6 - 8.2	6	6.56	1.15
Tail height, axil of pelvics	5.2 - 5.9	7	5.57	0.23	4.2 - 5.5	6	4.86	0.41
Pectoral insertion to sting origin	41.1 - 44.9	7	43.22	1.39	35.2 - 43.9	5	38.40	3.52
Cloaca origin to sting	43.6 - 48.6	7	45.83	1.74	41.1 - 46.6	5	44.00	2.59
Tail width, base of sting	2.5 - 2.9	7	2.73	0.11	1.8 - 2.7	6	2.29	0.30
Tail height, base of sting	2.3 - 2.7	7	2.52	0.13	2.0 - 2.6	6	2.24	0.20
Sting 1 length	14.3 - 16.5	7	15.29	0.79	4.7 - 19.4	3	12.69	7.39
Sting 2 length	x - x	7			20.6 - 20.6	1	20.65	
Snout preoral	21.0 - 22.7	7	22.09	0.67	20.0 - 22.6	6	21.75	0.97
Mouth width	7.0 - 7.9	7	7.43	0.33	6.5 - 8.3	6	7.35	0.60
Distance between nostrils	8.1 - 8.7	7	8.43	0.21	7.8 - 8.9	6	8.47	0.42
Interorbital width	12.1 - 13.3	7	12.86	0.42	11.5 - 15.4	6	13.68	1.52
Intereye width	21.7 - 25.8	7	23.54	1.26	19.2 - 22.5	6	21.02	1.28
Snout to maximum width	33.4 - 42.6	7	39.14	3.39	38.3 - 42.2	6	40.08	1.56
Eye diameter	3.6 - 4.1	7	3.83	0.16	3.4 - 4.0	6	3.67	0.19
Orbit diameter	5.8 - 7.4	7	6.16	0.56	5.6 - 6.1	6	5.86	0.21
Spiracle length	8.3 - 10.6	7	9.52	0.67	7.0 - 9.3	6	7.53	0.91
Interspiracular width	20.6 - 21.5	7	21.13	0.32	18.9 - 19.7	6	19.23	0.30
Orbit and spiracle length	11.0 - 12.3	7	11.63	0.45	9.9 - 11.2	6	10.45	0.52

...continued

Table 5.2.9c. continued.

Nostril length	4.0 - 4.6	7	4.25	0.21	4.1 - 5.0	6	4.64	0.33
Snout prenasal	15.6 - 17.7	7	16.58	0.80	14.8 - 17.6	6	16.52	0.99
Nasal curtain width	10.5 - 11.6	7	11.06	0.32	9.8 - 11.3	6	10.63	0.59
Nasal curtain length	5.3 - 6.3	7	5.60	0.38	5.0 - 6.1	6	5.64	0.39
End of orbit to pectoral insertion	60.6 - 65.2	7	63.01	1.77	60.0 - 65.7	6	62.26	2.22
Snout to origin of cloaca	80.0 - 87.4	7	82.81	2.36	77.2 - 82.0	6	79.74	2.12
Width, 1st gill slit	2.9 - 3.3	7	3.00	0.13	2.9 - 3.5	5	3.18	0.21
Width, 3rd gill slit	2.9 - 3.3	7	3.16	0.14	3.3 - 3.4	5	3.38	0.04
Width, 5th gill slit	2.0 - 2.5	7	2.22	0.17	2.2 - 2.4	5	2.30	0.09
Head length	44.7 - 48.4	7	46.66	1.09	44.3 - 46.6	5	45.74	0.87
Distance between 1st gill slits	19.5 - 21.1	7	20.44	0.67	19.5 - 21.3	5	20.53	0.76
Distance between 5th gill slits	12.6 - 13.4	7	12.87	0.25	13.0 - 13.8	5	13.32	0.32
Cloaca length	4.0 - 5.1	7	4.65	0.36	3.4 - 5.9	6	4.87	0.88
Clasper, postcloaca length	8.9 - 10.5	4	9.70	0.69	9.7 - 11.1	5	10.29	0.59
Clasper, length from pelvic axil	4.8 - 5.4	4	5.09	0.25	4.6 - 5.0	5	4.81	0.18

Table 5.2.10c. Counts and meristic values for *H. uarnak.*

	(F)		(G)	
	Range	N	Range	N
Oral papillae (floor)	4 - 5	7	4 - 4	1
Palate ridges	3 - 3	6	3 - 3	1
Upper tooth rows	n.a - n.a	7	n.a - n.a	1
Lower tooth rows	n.a - n.a	7	n.a - n.a	1
Total pectoral radials	147 - 154	2	145 - 152	4
Propterygial radials	61 - 63	2	59 - 62	4
Mesopterygial radials	19 - 20	2	18 - 21	4
Metapterygial radials	65 - 72	2	67 - 72	4
Total pelvic radials	25 - 27	2	27 - 29	4
Total vertebral segments	121 - 124	2	119 - 124	4
Monospondylous vertebrae	51 - 53	2	51 - 54	3
Prespine diplospondylous	68 - 73	2	65 - 74	3
Postspine diplospondylous	0 - 0	2	0 - 0	3

Table 5.2.11. Measurements in % of disc width, for *H. undulata* (Bleeker 1852). (A) BMNH 1867.11.28.156 (possible syntype of *T. undulata*); (B) CSIRO H5482.02, CSIRO H5483.01, CSIRO H5482.03 (nontype, males and a female, Sabah, Malaysia). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)			
		Range	N	Mean	S.D.
Disc width (mm)	264.6	358.0 - 456.0	3	414.67	50.77
Total length	n.a	n.a - n.a	3		
Disc length	274.5	100.9 - 102.5	3	101.60	0.84
Snout to pectoral insert	245.8	90.6 - 100.7	3	94.48	5.44
Disc thickness	27.5	11.2 - 12.1	3	11.68	0.46
Snout preorbital	69.0	27.7 - 29.0	3	28.50	0.70
Snout preorbital (horizontal)	62.7	26.2 - 27.9	3	27.23	0.88
Length pelvic-fin	54.7	19.1 - 19.9	2	19.48	0.53
Width across pelvic-fin base	36.8	12.3 - 13.6	3	12.72	0.76
Greatest width across pelvic-fins	24.3	n.a - n.a	3		
Cloaca origin to tail tip	n.a	n.a - n.a	3		
Tail width, axil of pelvics	19.9	7.4 - 7.7	3	7.56	0.17
Tail height, axil of pelvics	14.9	5.6 - 5.7	3	5.61	0.07
Pectoral insertion to sting origin	n.a	n.a - n.a	3		
Cloaca origin to sting	n.a	n.a - n.a	3		
Tail width, base of sting	n.a	2.5 - 2.6	2	2.57	0.05
Tail height, base of sting	n.a	2.4 - 2.5	2	2.49	0.06
Sting length	n.a	n.a - n.a	3		
Snout preoral	76.6	29.5 - 30.5	3	29.88	0.56
Mouth width	21.2	7.9 - 8.3	3	8.06	0.20
Distance between nostrils	25.9	10.0 - 10.5	3	10.29	0.28
Interorbital width	37.3	13.0 - 15.5	3	14.10	1.28
Intereye width	54.5	17.2 - 21.0	3	18.96	1.94
Snout to maximum width	116.9	44.8 - 46.3	3	45.46	0.74
Eye diameter	10.3	3.2 - 3.9	3	3.56	0.35
Orbit diameter	16.1	4.7 - 5.1	3	4.87	0.17
Spiracle length	22.2	6.7 - 7.1	3	6.94	0.20
Interspiracular width	55.6	17.7 - 20.6	3	19.03	1.47
Orbit and spiracle length	31.5	9.8 - 10.1	3	9.98	0.16

...continued

Table 5.2.11. continued.

Nostril length	9.6	4.4 - 4.7	3	4.58	0.12
Snout prenasal	58.4	22.6 - 23.8	3	23.14	0.62
Nasal curtain width	28.3	11.8 - 12.7	3	12.33	0.49
Nasal curtain length	12.4	5.7 - 6.1	3	5.96	0.24
End of orbit to pectoral insertion	165.1	59.4 - 60.5	3	60.07	0.60
Snout to origin of cloaca	231.1	83.3 - 85.5	3	84.41	1.07
Width, 1st gill slit	7.0	3.0 - 3.3	3	3.12	0.15
Width, 3rd gill slit	7.7	3.1 - 3.5	3	3.30	0.20
Width, 5th gill slit	7.3	2.2 - 2.4	3	2.29	0.10
Head length	138.2	51.3 - 53.1	3	52.09	0.92
Distance between 1st gill slits	57.3	20.2 - 21.0	3	20.45	0.45
Distance between 5th gill slits	34.8	12.4 - 13.0	3	12.73	0.30
Cloaca length	12.1	6.1 - 6.5	3	6.29	0.19
Clasper, postcloaca length	x	9.0 - 9.2	2	9.08	0.12
Clasper, length from pelvic axil	x	5.3 - 5.4	2	5.31	0.08

Table 5.2.12. Counts and meristic values for *H. undulata*. (*count by P. Last)

	(A)*	(B)	
		Range	N
Oral papillae (floor)	4	2 - 2	3
Palate ridges	n.a	3 - 3	3
Upper tooth rows	n.a	n.a - n.a	3
Lower tooth rows	n.a	n.a - n.a	3
Total pectoral radials	n.a	149 - 154	3
Propterygial radials	n.a	62 - 63	3
Mesopterygial radials	n.a	21 - 25	3
Metapterygial radials	n.a	65 - 69	3
Total pelvic radials	n.a	24 - 28	3
Total vertebral segments	n.a	112 - 112	1
Monospondylous vertebrae	n.a	46 - 49	3
Prespine diplospondylous	n.a	63 - 63	1
Postspine diplospondylous	n.a	0 - 0	1

Table 5.2.13. Measurements in % of disc width, for *H.* sp. A (typical 'leopard' form). (A) CAS 213280, CSIRO H635.02, CSIRO H3863.01, CSIRO H3863.02, CSIRO H4131.01, CSIRO H5478.01 (<500 mm DW); (B) CSIRO H2903.01, UMS MMKK136 (>500 mm DW). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(A)				(B)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	200.0 - 447.0	6	343.33	80.50	660.0 - 1105.0	2	882.50	314.66
Total length	362.0 - 466.5	5	417.71	37.36	325.2 - 325.2	1	325.15	
Disc length	89.9 - 100.8	6	94.17	3.86	86.1 - 90.1	2	88.10	2.88
Snout to pectoral insert	80.1 - 92.0	6	85.04	4.46	78.8 - 81.4	2	80.12	1.88
Disc thickness	9.0 - 12.7	6	11.44	1.38	10.6 - 13.6	2	12.09	2.10
Snout preorbital	21.4 - 26.8	6	23.82	2.04	21.8 - 22.5	2	22.12	0.49
Snout preorbital (horizontal)	20.4 - 24.1	6	21.94	1.50	20.3 - 21.5	2	20.90	0.85
Length pelvic-fin	17.1 - 19.0	6	17.98	0.70	17.7 - 18.1	2	17.89	0.24
Width across pelvic-fin base	11.0 - 13.4	6	11.88	0.88	10.8 - 10.8	2	10.81	0.06
Greatest width across pelvic-fins	19.5 - 33.6	5	24.77	5.24	22.6 - 32.3	2	27.43	6.85
Cloaca origin to tail tip	285.1 - 376.7	5	335.49	32.92	253.2 - 253.2	1	253.18	
Tail width, axil of pelvics	6.2 - 7.9	6	6.82	0.57	5.3 - 5.3	2	5.32	0.03
Tail height, axil of pelvics	5.1 - 6.0	6	5.41	0.33	4.6 - 4.6	2	4.64	0.01
Pectoral insertion to sting origin	39.1 - 41.5	5	40.36	1.07	34.1 - 34.1	1	34.09	
Cloaca origin to sting	41.9 - 44.3	5	43.01	0.93	40.6 - 40.6	1	40.61	
Tail width, base of sting	2.2 - 2.4	5	2.32	0.08	1.7 - 1.7	1	1.73	
Tail height, base of sting	2.5 - 2.8	5	2.64	0.14	1.9 - 1.9	1	1.88	
Sting length	12.4 - 15.4	5	14.13	1.30	n.a - n.a	2		
Snout preoral	22.6 - 27.6	6	24.39	1.93	21.5 - 23.3	2	22.43	1.29
Mouth width	7.2 - 9.9	6	8.00	0.97	6.5 - 7.2	2	6.84	0.46
Distance between nostrils	9.2 - 11.8	6	9.71	1.05	8.6 - 8.8	2	8.71	0.11
Interorbital width	13.1 - 21.5	6	16.50	2.78	12.6 - 13.1	2	12.85	0.38
Intereye width	18.1 - 31.1	6	23.23	4.31	16.3 - 16.8	2	16.53	0.36
Snout to maximum width	37.9 - 52.1	6	43.67	4.88	38.0 - 38.0	2	38.01	0.04
Eye diameter	2.6 - 4.6	6	3.27	0.72	1.8 - 1.9	2	1.83	0.11
Orbit diameter	4.6 - 7.0	6	5.20	0.94	3.5 - 4.0	2	3.73	0.34
Spiracle length	6.6 - 12.1	6	9.09	1.78	5.6 - 5.6	2	5.63	0.03
Interspiracular width	17.5 - 25.8	6	21.02	2.78	15.2 - 15.8	2	15.49	0.48
Orbit and spiracle length	9.6 - 14.3	6	11.07	1.72	7.7 - 8.2	2	7.94	0.41

...continued

Table 5.2.13. continued.

Nostril length	3.8 - 4.9	6	4.24	0.36	3.8 - 4.1	2	3.96	0.19
Snout prenasal	16.6 - 21.1	6	18.47	1.75	16.4 - 18.3	2	17.35	1.28
Nasal curtain width	10.2 - 14.0	6	11.31	1.40	10.2 - 10.8	2	10.48	0.46
Nasal curtain length	5.5 - 6.6	6	6.02	0.38	5.4 - 5.6	2	5.52	0.14
End of orbit to pectoral insertion	54.6 - 62.5	6	59.16	3.16	54.5 - 56.6	2	55.56	1.43
Snout to origin of cloaca	76.3 - 89.8	6	81.23	4.98	72.0 - 75.6	2	73.77	2.54
Width, 1st gill slit	2.8 - 3.3	6	2.99	0.17	2.8 - 3.1	2	2.97	0.23
Width, 3rd gill slit	2.9 - 3.3	6	3.11	0.18	3.0 - 3.3	2	3.16	0.19
Width, 5th gill slit	1.9 - 2.3	6	2.11	0.15	2.1 - 2.1	2	2.13	0.01
Head length	43.5 - 54.5	6	47.39	4.11	42.1 - 43.7	2	42.92	1.14
Distance between 1st gill slits	18.3 - 24.4	6	20.32	2.08	17.1 - 18.3	2	17.71	0.83
Distance between 5th gill slits	11.9 - 15.0	6	12.85	1.12	10.8 - 12.2	2	11.46	1.00
Cloaca length	3.7 - 5.4	6	4.75	0.63	4.3 - 6.3	2	5.30	1.46
Clasper, postcloaca length	9.5 - 9.5	1	9.49		x - x	2		
Clasper, length from pelvic axil	4.6 - 4.6	1	4.62		x - x	2		

Table 5.2.14. Counts and meristic values for *H.* sp. A.

	(A)		(B)	
	Range	N	Range	N
Oral papillae (floor)	4 - 4	3	n.a - n.a	2
Palate ridges	3 - 3	2	n.a - n.a	2
Upper tooth rows	n.a - n.a	1	28 - 28	1
Lower tooth rows	n.a - n.a	6	n.a - n.a	1
Total pectoral radials	152 - 158	4	n.a - n.a	2
Propterygial radials	60 - 65	4	n.a - n.a	2
Mesopterygial radials	20 - 23	4	n.a - n.a	2
Metapterygial radials	69 - 74	4	n.a - n.a	2
Total pelvic radials	24 - 31	4	n.a - n.a	2
Total vertebral segments	115 - 123	4	n.a - n.a	2
Monospondylous vertebrae	48 - 55	5	n.a - n.a	2
Prespine diplospondylous	62 - 70	4	n.a - n.a	2
Postspine diplospondylous	0 - 0	2	n.a - n.a	2

Table 5.2.15. Measurements in % of disc width, for *H.* sp. B. (BPBM 29480, BPBM 33201(1of2), BPBM 33201(2of2), MTUF 20642: females and a male, Persian Gulf, Kuwait). N is number of specimens from which means and standard deviations (S.D.) were taken.

	Range	N	Mean	S.D.
Disc width (mm)	151.0 - 414.0	4	284.00	112.12
Total length	302.8 - 337.7	3	316.76	18.51
Disc length	95.1 - 97.6	4	96.35	1.04
Snout to pectoral insert	85.4 - 87.1	4	86.36	0.70
Disc thickness	12.3 - 16.9	4	13.81	2.17
Snout preorbital	20.1 - 23.0	4	21.84	1.22
Snout preorbital (horizontal)	19.2 - 21.7	4	20.77	1.16
Length pelvic-fin	18.6 - 21.2	4	20.48	1.22
Width across pelvic-fin base	14.0 - 15.6	4	14.52	0.73
Greatest width across pelvic-fins	29.7 - 34.3	4	31.05	2.15
Cloaca origin to tail tip	224.4 - 257.8	3	237.82	17.67
Tail width, axil of pelvics	5.9 - 7.8	4	6.81	0.79
Tail height, axil of pelvics	4.6 - 5.5	4	4.97	0.38
Pectoral insertion to sting origin	30.8 - 34.7	4	32.56	1.76
Cloaca origin to sting	36.3 - 41.7	4	38.59	2.32
Tail width, base of sting	2.6 - 3.4	4	2.80	0.38
Tail height, base of sting	2.2 - 2.8	4	2.57	0.23
Sting 1 length	5.5 - 17.2	3	12.31	6.12
Sting 2 length	17.6 - 17.6	1	17.59	
Snout preoral	21.9 - 22.7	4	22.22	0.41
Mouth width	6.5 - 7.3	4	6.83	0.36
Distance between nostrils	8.1 - 8.8	4	8.35	0.30
Interorbital width	12.8 - 14.7	4	14.08	0.90
Intereye width	19.3 - 21.7	4	20.16	1.11
Snout to maximum width	39.2 - 42.6	4	40.71	1.54
Eye diameter	2.6 - 4.5	4	3.63	0.81
Orbit diameter	4.6 - 7.1	4	5.88	1.08
Spiracle length	6.4 - 7.3	4	6.77	0.37
Interspiracular width	18.3 - 20.7	4	19.04	1.14
Orbit and spiracle length	9.3 - 11.3	4	10.24	0.89

...continued

Table 5.2.15. continued.

Nostril length	3.4 - 4.4	4	4.00	0.46
Snout prenasal	16.5 - 17.3	4	16.82	0.37
Nasal curtain width	10.0 - 10.5	2	10.27	0.36
Nasal curtain length	5.9 - 6.8	4	6.20	0.39
End of orbit to pectoral insertion	60.2 - 64.3	4	61.89	1.83
Snout to origin of cloaca	78.4 - 80.4	4	79.31	1.02
Width, 1st gill slit	2.6 - 3.1	4	2.88	0.24
Width, 3rd gill slit	2.9 - 3.5	4	3.24	0.24
Width, 5th gill slit	2.0 - 2.6	4	2.26	0.25
Head length	44.9 - 47.8	4	46.06	1.26
Distance between 1st gill slits	20.3 - 22.0	4	21.04	0.79
Distance between 5th gill slits	12.9 - 14.4	4	13.43	0.67
Cloaca length	4.5 - 7.2	4	5.97	1.14
Clasper, postcloaca length	16.0 - 16.0	1	15.96	
Clasper, length from pelvic axil	11.0 - 11.0	1	10.97	

Table 5.2.16. Counts and meristic values for *H.* sp. B.

	Range	N
Oral papillae (floor)	2 - 2	1
Palate ridges	3 - 3	1
Upper tooth rows	n.a - n.a	1
Lower tooth rows	n.a - n.a	1
Total pectoral radials	125 - 129	4
Propterygial radials	48 - 52	4
Mesopterygial radials	17 - 20	4
Metapterygial radials	58 - 60	4
Total pelvic radials	25 - 29	4
Total vertebral segments	108 - 112	4
Monospondylous vertebrae	43 - 45	4
Prespine diplospondylous	63 - 68	4
Postspine diplospondylous	0 - 0	4

Table 5.2.17. Measurements in % of disc width, for *H.* sp. C. (CAS 29630, CAS 29646, LACM 38133-48(3of4), LACM 38133-48(4of4), LACM 38311-34(2of2), LACM 38312-27(1of2), LACM 38318-11(3of4), LACM 38318-11(4of4): males and females, Pakistan). N is number of specimens from which means and standard deviations (S.D.) were taken.

	Range	N	Mean	S.D.
Disc width (mm)	173.0 - 325.0	8	243.75	45.73
Total length	299.2 - 339.1	6	320.78	15.48
Disc length	88.8 - 95.2	8	92.04	2.04
Snout to pectoral insert	77.7 - 86.2	8	81.65	2.41
Disc thickness	9.2 - 14.1	8	11.79	1.68
Snout preorbital	20.5 - 23.4	8	21.63	0.97
Snout preorbital (horizontal)	19.0 - 21.7	8	20.01	1.11
Length pelvic-fin	16.6 - 20.5	8	19.36	1.27
Width across pelvic-fin base	11.7 - 14.7	8	12.70	0.88
Greatest width across pelvic-fins	27.5 - 35.6	7	30.47	3.09
Cloaca origin to tail tip	222.2 - 261.6	6	244.22	15.47
Tail width, axil of pelvics	6.5 - 7.9	8	6.90	0.46
Tail height, axil of pelvics	4.0 - 5.3	8	4.50	0.48
Pectoral insertion to sting origin	28.9 - 34.1	8	31.60	1.81
Cloaca origin to sting	33.9 - 39.1	8	35.66	1.73
Tail width, base of sting	2.1 - 2.6	8	2.29	0.18
Tail height, base of sting	2.1 - 2.8	8	2.38	0.18
Sting length	16.8 - 20.5	7	18.32	1.25
Snout preoral	20.5 - 23.9	8	22.16	1.08
Mouth width	6.0 - 7.1	8	6.71	0.39
Distance between nostrils	8.4 - 9.6	8	9.06	0.46
Interorbital width	11.2 - 13.8	8	12.12	0.85
Intereye width	17.0 - 20.7	8	18.35	1.39
Snout to maximum width	39.2 - 44.0	8	41.65	1.58
Eye diameter	3.0 - 4.3	8	3.58	0.37
Orbit diameter	5.3 - 7.0	8	6.26	0.54
Spiracle length	5.8 - 8.3	8	6.85	0.71
Interspiracular width	16.4 - 19.4	8	17.65	1.11
Orbit and spiracle length	9.6 - 11.3	8	10.28	0.58

...continued

Table 5.2.17. continued.

Nostril length	4.0 - 4.6	8	4.43	0.22
Snout prenasal	15.7 - 18.1	8	16.75	0.79
Nasal curtain width	9.5 - 10.9	8	10.25	0.57
Nasal curtain length	5.4 - 6.7	8	6.13	0.37
End of orbit to pectoral insertion	53.3 - 59.8	8	56.71	1.96
Snout to origin of cloaca	72.8 - 80.1	8	76.15	2.23
Width, 1st gill slit	2.7 - 3.3	8	3.04	0.23
Width, 3rd gill slit	3.0 - 3.5	8	3.22	0.17
Width, 5th gill slit	1.7 - 2.1	8	1.93	0.14
Head length	43.2 - 47.3	8	45.36	1.42
Distance between 1st gill slits	18.9 - 21.5	8	19.96	0.92
Distance between 5th gill slits	12.3 - 13.4	8	12.81	0.35
Cloaca length	3.6 - 4.9	8	4.15	0.39
Clasper, postcloaca length	9.2 - 10.0	3	9.55	0.43
Clasper, length from pelvic axil	4.8 - 5.7	3	5.39	0.55

Table 5.2.18. Counts and meristic values for *H.* sp. C.

	Range	N
Oral papillae (floor)	2 - 4	5
Palate ridges	3 - 3	1
Upper tooth rows	n.a - n.a	5
Lower tooth rows	n.a - n.a	5
Total pectoral radials	127 - 135	6
Propterygial radials	51 - 54	6
Mesopterygial radials	15 - 21	6
Metapterygial radials	58 - 62	6
Total pelvic radials	24 - 30	6
Total vertebral segments	102 - 111	6
Monospondylous vertebrae	41 - 47	6
Prespine diplospondylous	55 - 68	6
Postspine diplospondylous	0 - 0	6

Table 5.2.19. Measurements in % of disc width, for *H.* sp. D. (CAS 141048, LACM 38130-47(1of3), LACM 38130-47(2of3), LACM 38130-47(3of3), LACM 38131-43, MTUF 30005: males and females, Pakistan and India). N is number of specimens from which means and standard deviations (S.D.) were taken.

	Range	N	Mean	S.D.
Disc width (mm)	198.0 - 421.0	6	261.83	80.07
Total length	319.1 - 439.2	4	354.41	57.09
Disc length	92.5 - 98.6	6	95.68	2.37
Snout to pectoral insert	82.9 - 88.3	6	85.71	2.07
Disc thickness	10.6 - 15.6	6	12.82	1.64
Snout preorbital	20.4 - 23.5	6	21.31	1.28
Snout preorbital (horizontal)	17.7 - 22.4	6	19.55	1.67
Length pelvic-fin	18.5 - 22.3	6	20.39	1.68
Width across pelvic-fin base	14.3 - 15.6	6	14.88	0.57
Greatest width across pelvic-fins	29.4 - 35.8	4	33.05	2.74
Cloaca origin to tail tip	242.7 - 357.4	4	275.02	55.22
Tail width, axil of pelvics	7.0 - 8.8	6	7.90	0.56
Tail height, axil of pelvics	4.5 - 5.3	6	4.88	0.38
Pectoral insertion to sting origin	32.2 - 36.7	6	34.21	2.19
Cloaca origin to sting	36.9 - 44.0	6	39.81	2.90
Tail width, base of sting	2.6 - 3.0	6	2.79	0.15
Tail height, base of sting	2.4 - 2.9	6	2.62	0.19
Sting length	17.2 - 25.2	5	22.32	3.38
Snout preoral	20.5 - 23.6	5	22.18	1.30
Mouth width	6.5 - 7.5	6	7.06	0.35
Distance between nostrils	6.8 - 9.4	6	8.50	1.05
Interorbital width	12.5 - 14.1	6	12.90	0.60
Intereye width	17.8 - 22.1	6	19.85	1.44
Snout to maximum width	35.9 - 43.2	6	40.46	2.53
Eye diameter	3.4 - 4.5	6	3.91	0.34
Orbit diameter	4.8 - 7.4	6	6.50	0.88
Spiracle length	5.9 - 7.2	6	6.53	0.48
Interspiracular width	16.6 - 20.4	6	18.78	1.25
Orbit and spiracle length	8.9 - 11.4	6	10.31	0.85

...continued

Table 5.2.19. continued.

Nostril length	3.6 - 4.6	6	4.23	0.37
Snout prenasal	15.7 - 18.4	5	16.84	1.12
Nasal curtain width	9.1 - 11.2	6	10.50	0.78
Nasal curtain length	4.8 - 6.8	6	5.96	0.76
End of orbit to pectoral insertion	59.6 - 62.5	6	60.58	1.07
Snout to origin of cloaca	76.3 - 82.0	6	78.86	2.46
Width, 1st gill slit	2.7 - 3.3	6	2.96	0.20
Width, 3rd gill slit	3.0 - 3.3	6	3.14	0.10
Width, 5th gill slit	1.9 - 2.2	6	2.03	0.09
Head length	44.0 - 48.6	6	45.67	1.70
Distance between 1st gill slits	18.3 - 21.9	6	20.44	1.21
Distance between 5th gill slits	11.0 - 13.7	6	12.93	0.99
Cloaca length	4.1 - 6.2	6	4.93	0.79
Clasper, postcloaca length	9.2 - 11.6	4	10.13	1.06
Clasper, length from pelvic axil	4.8 - 6.0	4	5.46	0.55

Table 5.2.20. Counts and meristic values for *H.* sp. D.

	Range	N
Oral papillae (floor)	4 - 4	1
Palate ridges	3 - 3	1
Upper tooth rows	n.a - n.a	1
Lower tooth rows	n.a - n.a	1
Total pectoral radials	127 - 132	5
Propterygial radials	50 - 53	5
Mesopterygial radials	17 - 21	5
Metapterygial radials	57 - 60	5
Total pelvic radials	23 - 30	5
Total vertebral segments	111 - 121	4
Monospondylous vertebrae	44 - 55	5
Prespine diplospondylous	64 - 69	5
Postspine diplospondylous	0 - 0	5

Table 5.3.1a. Measurements in % of disc width, for *H. chaophraya* Monkolprasit & Roberts 1990. (A) RMNH 7452 (holotype of *T. polylepis*, immature male); (B) F 4190/1 (see Annandale 1910); (C) unregistered (see Annandale 1910); (D) MTUF 30233, MTUF 30203 (male and female; Ganges River, India). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)	(C)				(D)
				Range	N	Mean	S.D.
Disc width (mm)	301.0	1387.5	1410.0	450.0 - 494.0	2	472.00	31.11
Total length	345.5	n.a	n.a	302.6 - 330.9	2	316.76	19.98
Disc length	114.0	97.3	n.a	105.9 - 107.8	2	106.82	1.35
Snout to pectoral insert	n.a	n.a	n.a	93.0 - 95.6	2	94.30	1.84
Disc thickness	n.a	n.a	n.a	12.0 - 14.2	2	13.09	1.53
Snout preorbital	33.2	n.a	n.a	30.4 - 31.6	2	31.00	0.84
Snout preorbital (horizontal)	n.a	n.a	n.a	28.6 - 31.0	2	29.80	1.69
Length pelvic-fin	15.9	n.a	n.a	18.0 - 18.5	2	18.25	0.40
Width across pelvic-fin base	n.a	n.a	n.a	11.3 - 11.7	2	11.47	0.27
Greatest width across pelvic-fins	13.3	n.a	n.a	33.0 - 33.2	2	33.10	0.20
Cloaca origin to tail tip	248.5	n.a	n.a	218.0 - 240.9	2	229.43	16.20
Tail width, axil of pelvics	5.9	n.a	n.a	5.7 - 6.6	2	6.15	0.61
Tail height, axil of pelvics	n.a	n.a	n.a	4.1 - 4.9	2	4.53	0.59
Pectoral insertion to sting origin	n.a	n.a	n.a	n.a - n.a	2		
Cloaca origin to sting	n.a	n.a	n.a	36.2 - 37.3	2	36.75	0.73
Tail width, base of sting	n.a	n.a	n.a	1.9 - 2.0	2	1.97	0.10
Tail height, base of sting	n.a	n.a	n.a	2.2 - 2.3	2	2.25	0.11
Sting length	n.a	n.a	n.a	n.a - n.a	2		
Snout preoral	32.6	n.a	n.a	28.9 - 31.9	2	30.42	2.15
Mouth width	8.1	9.0	n.a	7.1 - 7.8	2	7.46	0.54
Distance between nostrils	11.5	n.a	n.a	10.4 - 11.0	2	10.70	0.42
Interorbital width	16.8	n.a	n.a	12.8 - 13.1	2	12.94	0.24
Intereye width	n.a	14.4	n.a	17.0 - 17.8	2	17.36	0.58
Snout to maximum width	47.2	n.a	n.a	41.2 - 42.1	2	41.66	0.66
Eye diameter	2.6	n.a	n.a	2.0 - 2.0	2	1.99	0.02
Orbit diameter	4.7	n.a	n.a	3.8 - 3.9	2	3.84	0.07
Spiracle length	8.6	n.a	n.a	6.3 - 6.9	2	6.62	0.46
Interspiracular width	18.6	n.a	n.a	16.4 - 17.6	2	16.96	0.86
Orbit and spiracle length	11.5	n.a	n.a	8.6 - 9.3	2	8.96	0.44

...continued

Table 5.3.1a. continued.

Nostril length	n.a	n.a	n.a	3.1 - 3.4	2	3.25	0.19
Snout prenasal	28.6	n.a	n.a	24.8 - 26.4	2	25.57	1.15
Nasal curtain width	n.a	n.a	n.a	10.4 - 11.5	2	10.99	0.79
Nasal curtain length	4.8	n.a	n.a	4.2 - 5.3	2	4.73	0.82
End of orbit to pectoral insertion	n.a	n.a	n.a	61.0 - 61.6	2	61.30	0.40
Snout to origin of cloaca	97.0	n.a	n.a	84.7 - 90.0	2	87.33	3.78
Width, 1st gill slit	2.5	n.a	n.a	2.7 - 2.9	2	2.81	0.13
Width, 3rd gill slit	3.1	n.a	n.a	3.0 - 3.4	2	3.23	0.30
Width, 5th gill slit	2.9	n.a	n.a	1.9 - 2.1	2	1.96	0.13
Head length	n.a	n.a	n.a	53.3 - 54.4	2	53.85	0.75
Distance between 1st gill slits	20.7	n.a	n.a	20.9 - 21.5	2	21.23	0.42
Distance between 5th gill slits	14.2	n.a	n.a	15.6 - 16.3	2	15.97	0.52
Cloaca length	n.a	n.a	n.a	3.3 - 6.6	2	4.98	2.35
Clasper, postcloaca length	n.a	n.a	n.a	8.3 - 8.3	1	8.27	
Clasper, length from pelvic axil	n.a	n.a	n.a	4.1 - 4.1	1	4.05	

Table 5.3.2a. Counts and meristic values for *H. chaophraya*. (*count by P. Last).

	(A)*	(B)	(C)	(D)	
				Range	N
Oral papillae (floor)	5	n.a	n.a	5 - 5	1
Palate ridges	n.a	n.a	n.a	n.a - n.a	1
Upper tooth rows	n.a	n.a	n.a	23 - 23	1
Lower tooth rows	n.a	n.a	n.a	23 - 23	1
Total pectoral radials	n.a	n.a	n.a	165 - 169	2
Propterygial radials	n.a	n.a	n.a	67 - 73	2
Mesopterygial radials	n.a	n.a	n.a	32 - 33	2
Metapterygial radials	n.a	n.a	n.a	63 - 66	2
Total pelvic radials	n.a	n.a	n.a	24 - 27	2
Total vertebral segments	n.a	n.a	n.a	115 - 121	2
Monospondylous vertebrae	n.a	n.a	n.a	55 - 57	2
Prespine diplospondylous	n.a	n.a	n.a	60 - 64	2
Postspine diplospondylous	n.a	n.a	n.a	0 - 0	2

Table 5.3.1b. Measurements in % of disc width, for *H. chaophraya* Monkolprasit & Roberts 1990. (E) CSIRO H2524.01 (nontype, female, Gilbert River, Queensland); (F) CSIRO H2503.01 (nontype, immature male, Pentecost River, Western Australia); (G) MTUF 30204, MTUF 30205, MTUF 30206 (nontype, males and a female, Chaophraya River). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(E)	(F)	(G)			
			Range	N	Mean	S.D.
Disc width (mm)	450.0	620.0	460.0 - 480.0	3	468.67	10.26
Total length	310.7	296.1	318.7 - 323.3	2	320.97	3.25
Disc length	105.8	101.6	105.2 - 108.3	3	107.21	1.73
Snout to pectoral insert	95.5	91.0	93.3 - 97.2	3	95.76	2.12
Disc thickness	10.7	9.4	10.0 - 11.7	3	10.94	0.88
Snout preorbital	28.0	27.0	30.5 - 32.8	3	31.71	1.17
Snout preorbital (horizontal)	27.2	25.9	29.1 - 31.2	3	30.47	1.15
Length pelvic-fin	18.7	19.0	16.9 - 19.2	3	18.25	1.20
Width across pelvic-fin base	12.2	11.3	11.5 - 11.9	3	11.70	0.22
Greatest width across pelvic-fins	24.4	27.2	30.2 - 32.1	3	31.37	1.00
Cloaca origin to tail tip	221.8	211.4	219.7 - 232.4	2	226.07	8.94
Tail width, axil of pelvics	6.5	5.3	5.2 - 5.6	3	5.41	0.24
Tail height, axil of pelvics	4.7	3.9	4.3 - 4.4	3	4.31	0.06
Pectoral insertion to sting origin	n.a	n.a	n.a - n.a	3		
Cloaca origin to sting	39.8	34.1	36.4 - 39.3	2	37.88	2.04
Tail width, base of sting	1.9	1.7	1.8 - 1.9	2	1.85	0.12
Tail height, base of sting	2.1	2.2	2.1 - 2.3	2	2.20	0.11
Sting length	11.9	13.9	12.8 - 13.5	2	13.17	0.52
Snout preoral	28.2	27.5	30.1 - 32.1	3	31.39	1.09
Mouth width	8.5	8.4	7.7 - 8.0	3	7.86	0.17
Distance between nostrils	11.0	11.7	9.9 - 10.8	3	10.41	0.44
Interorbital width	18.1	15.8	12.2 - 13.1	3	12.58	0.50
Intereye width	13.2	12.4	16.3 - 17.5	3	16.80	0.62
Snout to maximum width	34.2	41.6	42.7 - 45.6	3	43.72	1.60
Eye diameter	2.5	2.1	2.0 - 2.3	3	2.11	0.13
Orbit diameter	4.8	3.4	3.4 - 3.8	3	3.66	0.25
Spiracle length	6.5	5.5	7.0 - 7.3	3	7.11	0.15
Interspiracular width	17.5	15.6	16.2 - 16.7	3	16.40	0.25
Orbit and spiracle length	9.8	8.2	8.8 - 9.8	3	9.27	0.54

...continued

Table 5.3.1b. continued.

Nostril length	3.3	3.2	3.6 - 3.7	3	3.62	0.06
Snout prenasal	22.7	22.6	25.1 - 27.6	3	26.54	1.29
Nasal curtain width	12.3	12.1	10.7 - 11.3	3	11.05	0.34
Nasal curtain length	5.4	5.8	5.3 - 5.5	3	5.41	0.12
End of orbit to pectoral insertion	65.5	61.4	60.7 - 62.0	3	61.38	0.66
Snout to origin of cloaca	88.8	84.8	87.9 - 98.9	3	92.57	5.70
Width, 1st gill slit	3.0	3.5	3.1 - 3.2	3	3.11	0.04
Width, 3rd gill slit	3.3	4.0	2.9 - 3.3	3	3.13	0.18
Width, 5th gill slit	2.3	2.3	1.9 - 2.8	3	2.23	0.53
Head length	51.3	51.4	53.0 - 54.7	3	53.95	0.85
Distance between 1st gill slits	21.5	21.1	19.8 - 21.5	3	20.80	0.86
Distance between 5th gill slits	15.2	15.0	15.4 - 16.3	3	15.93	0.50
Cloaca length	4.4	5.0	3.4 - 4.4	3	3.93	0.51
Clasper, postcloaca length	x	8.4	8.5 - 9.9	2	9.22	1.02
Clasper, length from pelvic axil	x	4.1	4.6 - 4.8	2	4.67	0.15

Table 5.3.2b. Counts and meristic values for *H. chaophraya*.

	(E)	(F)	(G)	
			Range	N
Oral papillae (floor)	n.a	n.a	4 - 4	3
Palate ridges	n.a	n.a	n.a - n.a	3
Upper tooth rows	n.a	n.a	22 - 23	3
Lower tooth rows	n.a	n.a	19 - 21	3
Total pectoral radials	n.a	n.a	n.a - n.a	3
Propterygial radials	n.a	n.a	n.a - n.a	3
Mesopterygial radials	n.a	n.a	n.a - n.a	3
Metapterygial radials	n.a	n.a	n.a - n.a	3
Total pelvic radials	n.a	n.a	n.a - n.a	3
Total vertebral segments	n.a	n.a	n.a - n.a	3
Monospondylous vertebrae	n.a	n.a	n.a - n.a	3
Prespine diplospondylous	n.a	n.a	n.a - n.a	3
Postspine diplospondylous	n.a	n.a	n.a - n.a	3

Table 5.3.1c. Measurements in % of disc width, for *H. chaophraya* Monkolprasit & Roberts 1990. (H) SMKK SKN10-15697 (nontype, maturing male, Sandakan fish market, Sabah; tail only saved); (I) SMKK BFT1-697 (nontype, female, Padas River, Sabah); (J) CSIRO H5283.01, SMKK KTG2-23397, SMKK KTG3-20497, SMKK KTG7-21096, UMS MMKG1 (nontype, males and a female, Kinabatangan River, Sabah). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(H)	(I)	(J)			
			Range	N	Mean	S.D.
Disc width (mm)	1210.0	605.0	372.0 - 545.0	5	483.80	69.40
Total length	216.9	262.0	283.1 - 323.4	2	303.25	28.48
Disc length	n.a	106.9	106.5 - 113.2	4	109.08	2.89
Snout to pectoral insert	n.a	95.4	78.4 - 102.8	5	94.35	9.32
Disc thickness	n.a	7.9	8.6 - 13.2	3	10.33	2.50
Snout preorbital	n.a	32.9	26.5 - 34.3	5	31.65	3.01
Snout preorbital (horizontal)	n.a	31.5	25.8 - 34.0	5	30.96	3.08
Length pelvic-fin	n.a	19.9	13.4 - 20.5	5	18.04	2.76
Width across pelvic-fin base	n.a	11.4	9.6 - 12.3	5	11.48	1.07
Greatest width across pelvic-fins	n.a	n.a	27.0 - 27.0	2	27.01	0.02
Cloaca origin to tail tip	n.a	172.6	192.8 - 232.3	2	212.57	27.94
Tail width, axil of pelvics	n.a	6.8	5.3 - 6.5	5	5.89	0.42
Tail height, axil of pelvics	n.a	4.1	3.8 - 4.7	5	4.29	0.36
Pectoral insertion to sting origin	n.a	n.a	n.a - n.a	5		
Cloaca origin to sting	n.a	36.4	31.8 - 38.8	3	35.44	3.48
Tail width, base of sting	n.a	2.0	2.4 - 2.4	3	2.40	0.03
Tail height, base of sting	n.a	2.1	2.3 - 2.6	3	2.48	0.14
Sting length	n.a	n.a	11.6 - 18.0	2	14.79	4.56
Snout preoral	n.a	33.3	26.3 - 34.6	5	32.08	3.36
Mouth width	n.a	7.7	6.2 - 8.4	5	7.66	0.90
Distance between nostrils	n.a	10.7	8.5 - 11.4	5	10.45	1.13
Interorbital width	n.a	11.4	11.1 - 13.8	5	12.70	0.99
Intereye width	n.a	15.6	15.4 - 18.8	5	16.96	1.25
Snout to maximum width	n.a	42.5	32.6 - 50.0	4	41.99	7.19
Eye diameter	n.a	1.9	1.8 - 2.2	5	1.97	0.17
Orbit diameter	n.a	3.3	3.2 - 4.1	5	3.61	0.33
Spiracle length	n.a	6.3	5.3 - 7.0	5	6.46	0.67
Interspiracular width	n.a	15.1	14.5 - 17.4	5	15.83	1.08
Orbit and spiracle length	n.a	9.0	7.8 - 10.2	5	9.39	0.98

...continued

Table 5.3.1c. continued.

Nostril length	n.a	3.3	2.8 - 3.7	5	3.48	0.37
Snout prenasal	n.a	28.2	22.3 - 29.0	5	26.91	2.70
Nasal curtain width	n.a	11.2	8.8 - 12.4	5	11.10	1.39
Nasal curtain length	n.a	5.3	4.2 - 5.9	5	5.30	0.70
End of orbit to pectoral insertion	n.a	60.7	49.4 - 66.1	5	60.00	6.26
Snout to origin of cloaca	n.a	89.4	74.3 - 94.7	5	87.62	7.85
Width, 1st gill slit	n.a	2.8	2.2 - 3.0	5	2.69	0.33
Width, 3rd gill slit	n.a	3.0	2.5 - 3.2	5	2.96	0.27
Width, 5th gill slit	n.a	1.9	1.4 - 2.0	5	1.82	0.22
Head length	n.a	54.5	45.1 - 58.0	5	53.83	5.05
Distance between 1st gill slits	n.a	20.1	17.0 - 21.4	5	20.32	1.86
Distance between 5th gill slits	n.a	15.1	12.7 - 15.8	5	15.08	1.32
Cloaca length	n.a	4.8	3.1 - 5.3	5	3.90	0.86
Clasper, postcloaca length	n.a	x	7.6 - 9.5	4	8.52	0.84
Clasper, length from pelvic axil	n.a	x	4.1 - 4.8	4	4.44	0.29

Table 5.3.2c. Counts and meristic values for *H. chaophraya*.

	(H)	(I)	(J)	
			Range	N
Oral papillae (floor)	n.a	n.a	4 - 4	1
Palate ridges	n.a	n.a	n.a - n.a	5
Upper tooth rows	n.a	n.a	n.a - n.a	6
Lower tooth rows	n.a	n.a	n.a - n.a	7
Total pectoral radials	n.a	n.a	167 - 168	2
Propterygial radials	n.a	n.a	69 - 69	1
Mesopterygial radials	n.a	n.a	34 - 36	1
Metapterygial radials	n.a	n.a	63 - 65	1
Total pelvic radials	n.a	n.a	24 - 24	1
Total vertebral segments	n.a	n.a	116 - 116	1
Monospondylous vertebrae	n.a	n.a	54 - 54	1
Prespine diplospondylous	n.a	n.a	62 - 62	1
Postspine diplospondylous	n.a	n.a	0 - 0	1

Table 5.3.3a. Measurements in % of disc width, for *H. granulata* (Macleay 1883). (A) AMS I9763 (holotype, female); (B) BMNH 1879.5.22.105 (holotype of *T. ponapensis*, neonate female); (C) CAS 52032 (nontype, female, Palau); (D) SUML JPAG207 (nontype, female, Buktol Island, Philippines); (E) SMF 4747 (nontype, immature male, Maldives). (*measurements by P. Last).

	(A)	(B)*	(C)	(D)	(E)*
Disc width (mm)	331.0	184.0	268.0	300.0	304.0
Total length	264.0	286.4	281.0	n.a	276.6
Disc length	107.6	107.9	106.7	106.3	107.6
Snout to pectoral insert	93.5	95.8	n.a	92.6	94.4
Disc thickness	10.9	14.1	n.a	15.1	14.1
Snout preorbital	22.6	21.9	25.0	23.2	21.7
Snout preorbital (horizontal)	21.7	19.1	n.a	21.3	n.a
Length pelvic-fin	22.8	18.5	18.3	22.5	24.0
Width across pelvic-fin base	13.3	13.2	n.a	14.4	14.8
Greatest width across pelvic-fins	n.a	10.2	17.2	38.2	n.a
Cloaca origin to tail tip	176.4	n.a	187.3	n.a	187.5
Tail width, axil of pelvics	9.7	8.6	8.2	10.5	n.a
Tail height, axil of pelvics	5.5	7.1	n.a	7.2	6.9
Pectoral insertion to sting origin	45.8	47.6	n.a	n.a	n.a
Cloaca origin to sting	51.9	51.0	53.4	n.a	56.3
Tail width, base of sting	2.8	3.8	n.a	n.a	4.2
Tail height, base of sting	2.7	3.7	n.a	n.a	3.8
Sting 1 length	n.a	22.9	n.a	n.a	n.a
Sting 2 length	n.a	n.a	n.a	n.a	n.a
Snout preoral	24.1	20.9	21.6	22.1	24.3
Mouth width	8.1	9.2	9.0	7.9	8.5
Distance between nostrils	9.7	n.a	9.7	9.2	11.2
Interorbital width	13.2	16.5	13.1	13.8	17.4
Intereye width	20.6	24.7	n.a	26.9	21.7
Snout to maximum width	41.7	48.6	42.2	50.7	49.7
Eye diameter	4.8	6.0	5.2	4.4	5.3
Orbit diameter	8.3	7.8	6.7	6.4	7.4
Spiracle length	7.0	12.4	9.0	8.0	7.0
Interspiracular width	20.2	25.5	23.9	21.8	21.4
Orbit and spiracle length	12.3	14.0	n.a	12.2	11.6

... continued

Table 5.3.3a. continued.

Nostril length	3.6	4.9	n.a	4.6	4.9
Snout prenasal	18.7	16.1	15.7	17.2	18.1
Nasal curtain width	10.2	n.a	n.a	12.0	n.a
Nasal curtain length	4.9	5.5	6.0	5.6	5.9
End of orbit to pectoral insertion	65.2	69.3	n.a	66.5	n.a
Snout to origin of cloaca	87.6	91.9	88.8	89.3	88.2
Width, 1st gill slit	3.5	4.1	n.a	4.0	4.1
Width, 3rd gill slit	4.2	4.7	n.a	4.4	n.a
Width, 5th gill slit	2.7	3.2	n.a	3.1	2.7
Head length	52.6	53.2	n.a	51.2	53.0
Distance between 1st gill slits	22.2	26.3	23.5	22.0	24.3
Distance between 5th gill slits	14.6	17.8	15.3	14.7	16.1
Cloaca length	6.8	5.7	n.a	4.1	n.a
Clasper, postcloaca length	x	x	x	x	n.a
Clasper, length from pelvic axil	x	x	x	x	n.a

Table 5.3.4a. Counts and meristic values for *H. granulata*. (*counts by P. Last).

	(A)	(B)*	(C)	(D)	(E)*
Oral papillae (floor)	2	4	n.a	n.a	4
Palate ridges	n.a	n.a	n.a	n.a	n.a
Upper tooth rows	20	n.a	n.a	n.a	n.a
Lower tooth rows	25	n.a	n.a	n.a	n.a
Total pectoral radials	145-146	n.a	n.a	146	n.a
Propterygial radials	64	n.a	n.a	65	n.a
Mesopterygial radials	18-20	n.a	n.a	17-18	n.a
Metapterygial radials	62-63	n.a	n.a	63-64	n.a
Total pelvic radials	33	n.a	n.a	30-33	n.a
Total vertebral segments	143	n.a	n.a	n.a	n.a
Monospondylous vertebrae	51	n.a	n.a	52	n.a
Prespine diplospondylous	92	n.a	n.a	n.a	n.a
Postspine diplospondylous	0	n.a	n.a	n.a	n.a

Table 5.3.3b. Measurements in % of disc width, for *H. granulata* (Macleay 1883). (F) MTUF 26903, MTUF 26906 (nontype, females, <500 mm DW, Maldives); (G) MTUF 26700, MTUF 26703, MTUF 26719 (nontype, males and a female, >500 mm DW, Maldives). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(F)				(G)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	148.0 - 230.0	2	189.00	57.98	686.0 - 780.0	3	717.67	53.98
Total length	265.2 - 297.3	2	281.26	22.68	211.1 - 228.9	2	219.96	12.59
Disc length	106.5 - 111.5	2	109.00	3.51	103.9 - 107.4	3	105.59	1.71
Snout to pectoral insert	92.4 - 96.7	2	94.58	3.03	91.6 - 94.0	3	92.62	1.23
Disc thickness	14.3 - 16.4	2	15.38	1.46	15.3 - 23.1	3	18.52	4.05
Snout preorbital	21.7 - 22.4	2	22.07	0.47	21.4 - 23.6	3	22.33	1.16
Snout preorbital (horizontal)	19.2 - 19.3	2	19.23	0.10	19.4 - 22.5	3	20.90	1.56
Length pelvic-fin	22.1 - 22.7	2	22.43	0.42	20.2 - 23.3	3	21.53	1.61
Width across pelvic-fin base	11.6 - 13.3	2	12.48	1.17	13.4 - 14.4	3	14.02	0.51
Greatest width across pelvic-fins	35.9 - 36.8	2	36.36	0.64	31.6 - 39.0	2	35.31	5.26
Cloaca origin to tail tip	175.4 - 204.7	2	190.03	20.74	126.1 - 145.9	2	136.00	14.07
Tail width, axil of pelvics	9.1 - 9.8	2	9.45	0.45	8.5 - 10.5	3	9.30	1.05
Tail height, axil of pelvics	7.5 - 8.2	2	7.86	0.47	6.5 - 6.8	3	6.69	0.15
Pectoral insertion to sting origin	46.8 - 52.9	2	49.82	4.31	38.8 - 38.8	1	38.79	
Cloaca origin to sting	50.2 - 55.9	2	53.04	4.01	47.7 - 47.7	1	47.74	
Tail width, base of sting	3.5 - 3.7	2	3.56	0.14	2.6 - 2.7	2	2.65	0.02
Tail height, base of sting	3.4 - 3.7	2	3.54	0.22	2.4 - 2.7	2	2.56	0.25
Sting 1 length	7.6 - 24.3	2	15.96	11.86	23.3 - 23.9	2	23.60	0.36
Sting 2 length	x - x	2			x - x	2		
Snout preoral	22.2 - 24.7	2	23.46	1.82	19.9 - 23.4	2	21.65	2.42
Mouth width	8.1 - 8.6	2	8.35	0.38	8.2 - 8.2	2	8.19	0.03
Distance between nostrils	9.5 - 9.5	2	9.49	0.05	10.3 - 11.6	3	11.01	0.64
Interorbital width	14.5 - 16.3	2	15.37	1.25	14.3 - 15.5	3	15.07	0.67
Intereye width	27.9 - 29.6	2	28.72	1.18	22.8 - 23.0	3	22.93	0.14
Snout to maximum width	42.6 - 45.7	2	44.16	2.19	45.1 - 47.2	3	45.92	1.16
Eye diameter	5.0 - 5.8	2	5.39	0.61	3.1 - 3.4	3	3.23	0.19
Orbit diameter	7.4 - 8.1	2	7.75	0.51	5.6 - 7.2	3	6.52	0.86
Spiracle length	10.8 - 12.0	2	11.39	0.80	6.7 - 8.2	3	7.29	0.84
Interspiracular width	23.0 - 25.6	2	24.27	1.86	19.5 - 21.2	3	20.28	0.84
Orbit and spiracle length	14.2 - 17.1	2	15.66	2.03	11.1 - 11.9	3	11.36	0.46

...continued

Table 5.3.3b. continued.

Nostril length	4.7 - 5.5	2	5.08	0.61	4.7 - 5.1	3	4.86	0.19
Snout prenasal	16.9 - 17.6	2	17.22	0.49	14.7 - 17.4	3	16.35	1.42
Nasal curtain width	11.3 - 12.7	2	11.99	0.97	12.0 - 12.6	3	12.33	0.33
Nasal curtain length	6.1 - 7.2	2	6.67	0.82	5.8 - 7.1	3	6.44	0.66
End of orbit to pectoral insertion	68.5 - 77.4	2	72.98	6.30	64.6 - 66.2	3	65.25	0.80
Snout to origin of cloaca	89.9 - 92.6	2	91.23	1.95	82.9 - 87.8	3	85.23	2.43
Width, 1st gill slit	3.5 - 3.9	2	3.68	0.27	3.6 - 4.0	3	3.84	0.20
Width, 3rd gill slit	4.1 - 4.4	2	4.22	0.18	4.1 - 4.5	3	4.30	0.19
Width, 5th gill slit	2.2 - 2.4	2	2.33	0.14	2.8 - 3.1	3	2.94	0.19
Head length	50.4 - 55.8	2	53.09	3.80	50.7 - 53.8	3	51.99	1.59
Distance between 1st gill slits	22.6 - 24.1	2	23.34	1.10	23.5 - 24.5	3	24.09	0.50
Distance between 5th gill slits	15.1 - 17.7	2	16.40	1.79	15.6 - 17.2	3	16.55	0.85
Cloaca length	4.6 - 4.9	2	4.71	0.22	5.5 - 7.7	3	6.70	1.12
Clasper, postcloaca length	x - x	2			22.8 - 24.1	2	23.44	0.95
Clasper, length from pelvic axil	x - x	2			20.1 - 20.6	2	20.34	0.36

Table 5.3.4b. Counts and meristic values for *H. granulata*.

	(F)		(G)	
	Range	N	Range	N
Oral papillae (floor)	2 - 2	1	n.a - n.a	3
Palate ridges	3 - 3	1	n.a - n.a	3
Upper tooth rows	n.a - n.a	2	23 - 23	1
Lower tooth rows	21 - 21	1	25 - 26	1
Total pectoral radials	145 - 146	1	n.a - n.a	3
Propterygial radials	64 - 64	1	n.a - n.a	3
Mesopterygial radials	18 - 19	1	n.a - n.a	3
Metapterygial radials	63 - 63	1	n.a - n.a	3
Total pelvic radials	28 - 29	1	n.a - n.a	3
Total vertebral segments	136 - 136	1	n.a - n.a	3
Monospondylous vertebrae	43 - 43	1	n.a - n.a	3
Prespine diplospondylous	93 - 93	1	n.a - n.a	3
Postspine diplospondylous	0 - 0	1	n.a - n.a	3

Table 5.3.3c. Measurements in % of disc width, for *H. granulata* (Macleay 1883). (CSIRO CA1255, CSIRO H962.01, CSIRO H2751.01, CSIRO H3864.01, CSIRO H4417.01, NTM S10718.062, QM I5879, QM I20184: males and females, Australia). N is number of specimens from which means and standard deviations (S.D.) were taken.

	Range	N	Mean	S.D.
Disc width (mm)	142.0 - 326.0	8	279.50	63.57
Total length	235.2 - 290.9	7	269.37	19.82
Disc length	102.1 - 109.4	8	106.90	2.56
Snout to pectoral insert	89.7 - 96.7	8	93.08	2.64
Disc thickness	12.9 - 15.8	8	13.82	1.02
Snout preorbital	18.6 - 25.2	8	22.16	2.00
Snout preorbital (horizontal)	17.7 - 22.1	8	20.07	1.57
Length pelvic-fin	19.2 - 23.9	8	21.97	1.75
Width across pelvic-fin base	11.8 - 16.3	8	13.58	1.29
Greatest width across pelvic-fins	30.1 - 35.6	3	33.03	2.77
Cloaca origin to tail tip	149.5 - 200.7	7	181.39	18.35
Tail width, axil of pelvics	6.3 - 10.7	8	8.92	1.42
Tail height, axil of pelvics	5.8 - 8.8	8	6.87	0.94
Pectoral insertion to sting origin	35.3 - 48.7	8	42.72	4.44
Cloaca origin to sting	40.7 - 51.0	7	45.48	3.53
Tail width, base of sting	2.8 - 4.1	8	3.40	0.48
Tail height, base of sting	3.0 - 3.7	8	3.33	0.21
Sting 1 length	3.6 - 28.6	8	19.81	9.37
Sting 2 length	25.3 - 25.3	1	25.35	
Snout preoral	20.3 - 26.0	8	22.89	1.69
Mouth width	7.0 - 9.0	8	8.15	0.59
Distance between nostrils	8.8 - 11.1	8	9.56	0.70
Interorbital width	12.7 - 17.9	8	13.97	1.66
Intereye width	21.5 - 26.2	8	24.90	1.67
Snout to maximum width	42.4 - 51.5	8	45.84	2.83
Eye diameter	4.1 - 6.1	8	4.53	0.68
Orbit diameter	6.1 - 9.4	8	7.12	1.10
Spiracle length	7.0 - 11.4	8	8.49	1.54
Interspiracular width	21.2 - 24.6	8	22.54	1.13
Orbit and spiracle length	11.7 - 14.6	8	12.66	1.15

...continued

Table 5.3.3c. continued.

Nostril length	4.1 - 5.4	8	4.85	0.42
Snout prenasal	16.5 - 20.1	8	17.81	1.06
Nasal curtain width	0.0 - 12.7	8	8.82	5.46
Nasal curtain length	5.6 - 6.5	8	6.14	0.36
End of orbit to pectoral insertion	63.4 - 73.9	8	69.01	3.76
Snout to origin of cloaca	84.4 - 91.7	8	87.54	2.35
Width, 1st gill slit	3.6 - 4.4	8	3.89	0.25
Width, 3rd gill slit	3.7 - 4.6	8	4.21	0.33
Width, 5th gill slit	2.5 - 3.3	8	2.93	0.25
Head length	49.2 - 53.2	8	51.63	1.32
Distance between 1st gill slits	20.8 - 23.9	8	22.89	0.94
Distance between 5th gill slits	13.9 - 15.9	8	15.02	0.59
Cloaca length	4.1 - 7.1	8	5.45	0.94
Clasper, postcloaca length	9.5 - 20.0	5	12.41	4.27
Clasper, length from pelvic axil	5.4 - 7.5	5	6.56	0.80

Table 5.3.4c. Counts and meristic values for *H. granulata.*

	Range	N
Oral papillae (floor)	4 - 7	2
Palate ridges	5 - 5	1
Upper tooth rows	n.a - n.a	8
Lower tooth rows	n.a - n.a	8
Total pectoral radials	142 - 149	4
Propterygial radials	63 - 67	4
Mesopterygial radials	14 - 21	4
Metapterygial radials	61 - 68	4
Total pelvic radials	23 - 32	4
Total vertebral segments	137 - 144	5
Monospondylous vertebrae	48 - 52	4
Prespine diplospondylous	86 - 92	4
Postspine diplospondylous	0 - 3	3

Table 5.3.5a. Measurements in % of disc width, for *H. pastinacoides* (Bleeker 1852). (A) BMNH 1867.11.28.161 (holotype, female); (B) BMNH 1867.11.28.155 (holotype of *T. pareh*, female); (C) CAS 213285 (nontype, female, Thailand); (D) CSIRO H4426.01, NMV A914 (nontype, male and female, Java). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)*	(C)	(D)			
				Range	N	Mean	S.D.
Disc width (mm)	156.0	436.0	227.0	165.0 - 427.0	2	296.00	185.26
Total length	n.a	243.6	365.6	297.4 - 297.4	1	297.42	
Disc length	101.3	103.2	100.4	97.2 - 103.0	2	100.11	4.13
Snout to pectoral insert	90.5	91.7	90.0	84.5 - 93.7	2	89.09	6.45
Disc thickness	11.2	n.a	13.2	13.6 - 13.9	2	13.76	0.25
Snout preorbital	24.2	23.3	22.3	21.0 - 24.0	2	22.50	2.13
Snout preorbital (horizontal)	22.0	n.a	20.8	20.5 - 22.3	2	21.39	1.22
Length pelvic-fin	22.6	24.8	23.8	20.0 - 22.3	2	21.16	1.59
Width across pelvic-fin base	15.7	n.a	15.6	15.4 - 17.1	2	16.25	1.16
Greatest width across pelvic-fins	34.9	n.a	34.8	34.4 - 39.0	2	36.72	3.28
Cloaca origin to tail tip	n.a	n.a	282.4	219.8 - 219.8	1	219.81	
Tail width, axil of pelvics	7.5	7.8	7.7	7.5 - 9.7	2	8.60	1.54
Tail height, axil of pelvics	5.1	5.3	5.0	4.9 - 5.8	2	5.40	0.64
Pectoral insertion to sting origin	n.a	44.3	37.7	37.7 - 37.7	1	37.67	
Cloaca origin to sting	n.a	n.a	43.5	42.4 - 42.4	1	42.44	
Tail width, base of sting	n.a	2.4	2.7	2.8 - 2.8	1	2.77	
Tail height, base of sting	n.a	2.6	2.7	2.6 - 2.6	1	2.57	
Sting length	n.a	n.a	23.2	n.a - n.a	2		
Snout preoral	24.9	23.1	23.5	21.3 - 25.3	2	23.27	2.82
Mouth width	8.9	7.9	6.6	6.1 - 8.0	2	7.06	1.40
Distance between nostrils	8.3	8.1	8.2	7.4 - 8.6	2	8.00	0.89
Interorbital width	15.0	n.a	13.4	13.9 - 14.2	2	14.09	0.22
Intereye width	22.3	n.a	21.0	18.6 - 21.4	2	20.00	2.00
Snout to maximum width	39.8	45.9	40.5	40.1 - 42.1	2	41.09	1.42
Eye diameter	5.0	3.6	4.6	2.7 - 4.8	2	3.75	1.52
Orbit diameter	6.7	4.9	7.0	4.0 - 7.6	2	5.80	2.48
Spiracle length	8.5	7.8	6.6	6.5 - 7.2	2	6.87	0.49
Interspiracular width	20.9	n.a	19.6	16.3 - 20.3	2	18.29	2.81
Orbit and spiracle length	11.6	9.8	10.9	8.3 - 11.9	2	10.12	2.52

...continued

Table 5.3.5a. continued.

Nostril length	3.2	4.6	4.0	3.8 - 4.1	2	3.95	0.15
Snout prenasal	18.4	17.8	17.9	16.9 - 18.7	2	17.81	1.25
Nasal curtain width	9.4	10.1	10.1	9.4 - 9.4	2	9.43	0.01
Nasal curtain length	5.1	5.9	5.6	4.1 - 5.5	2	4.80	1.00
End of orbit to pectoral insertion	62.0	63.1	63.3	60.7 - 64.1	2	62.39	2.37
Snout to origin of cloaca	n.a	n.a	83.2	77.6 - 87.7	2	82.64	7.10
Width, 1st gill slit	2.9	n.a	3.0	2.8 - 3.3	2	3.05	0.32
Width, 3rd gill slit	3.4	n.a	3.3	3.2 - 3.4	2	3.30	0.16
Width, 5th gill slit	2.0	n.a	2.1	1.9 - 2.2	2	2.05	0.25
Head length	50.0	n.a	47.0	44.6 - 51.1	2	47.83	4.61
Distance between 1st gill slits	22.3	n.a	22.6	20.7 - 23.0	2	21.88	1.64
Distance between 5th gill slits	14.8	n.a	13.4	13.6 - 15.3	2	14.45	1.24
Cloaca length	n.a	n.a	4.8	5.1 - 6.0	2	5.56	0.59
Clasper, postcloaca length	x	x	x	13.9 - 13.9	1	13.88	
Clasper, length from pelvic axil	x	x	x	8.7 - 8.7	1	8.74	

Table 5.3.6a. Counts and meristic values for *H. pastinacoides*. (*counts by P. Last).

	(A)*	(B)*	(C)	(D)	
				Range	N
Oral papillae (floor)	4	4	n.a	2 - 2	1
Palate ridges	3	n.a	n.a	3 - 3	1
Upper tooth rows	n.a	n.a	n.a	23 - 23	1
Lower tooth rows	n.a	n.a	n.a	27 - 27	1
Total pectoral radials	n.a	n.a	n.a	n.a - n.a	2
Propterygial radials	n.a	n.a	n.a	n.a - n.a	2
Mesopterygial radials	n.a	n.a	n.a	n.a - n.a	2
Metapterygial radials	n.a	n.a	n.a	n.a - n.a	2
Total pelvic radials	n.a	n.a	n.a	n.a - n.a	2
Total vertebral segments	n.a	n.a	n.a	n.a - n.a	2
Monospondylous vertebrae	n.a	n.a	n.a	n.a - n.a	2
Prespine diplospondylous	n.a	n.a	n.a	n.a - n.a	2
Postspine diplospondylous	n.a	n.a	n.a	n.a - n.a	2

Table 5.3.5b. Measurements in % of disc width, for *H. pastinacoides* (Bleeker 1852). (E) CSIRO H5471.01, CSIRO H5479.03, CSIRO H5479.13, CSIRO H5479.14, CSIRO H5479.15, CSIRO H5479.12, CSIRO H5480.02, CSIRO H5615.01, CSIRO H5615.02, CSIRO H5618.01, UMS MMSK7, UMS MMSK39, UMS MMSK40, UMS MMSK(26/3B) (nontype, males and females, Sabah); (F) CSIRO H4424.01, CSIRO H4424.02, CSIRO H4424.03 (nontype, females, Sarawak). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(E)				(F)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	163.0 - 945.0	14	405.79	194.08	292.0 - 341.0	3	313.33	25.11
Total length	322.5 - 386.3	3	364.27	36.22	342.0 - 372.1	2	357.08	21.30
Disc length	93.9 - 104.8	14	97.70	2.70	97.4 - 100.7	3	99.07	1.65
Snout to pectoral insert	83.3 - 89.9	13	86.11	1.64	86.0 - 88.8	3	87.72	1.48
Disc thickness	12.1 - 14.5	13	13.18	0.81	10.7 - 11.7	3	11.37	0.54
Snout preorbital	19.1 - 29.1	14	22.48	2.25	21.7 - 22.4	3	22.04	0.36
Snout preorbital (horizontal)	18.2 - 28.0	14	21.02	2.32	19.8 - 20.9	3	20.24	0.58
Length pelvic-fin	16.4 - 23.0	13	20.93	1.72	20.1 - 22.6	3	21.17	1.29
Width across pelvic-fin base	12.6 - 15.8	13	14.94	0.82	14.3 - 15.7	3	15.09	0.70
Greatest width across pelvic-fins	33.3 - 40.9	4	37.70	3.21	32.9 - 36.2	3	34.75	1.72
Cloaca origin to tail tip	242.9 - 303.9	3	282.73	34.51	262.2 - 290.1	2	276.12	19.72
Tail width, axil of pelvics	6.2 - 9.0	14	7.70	0.62	7.3 - 8.3	3	7.79	0.54
Tail height, axil of pelvics	3.3 - 6.0	14	4.97	0.60	4.9 - 5.6	3	5.18	0.39
Pectoral insertion to sting origin	34.3 - 43.8	12	38.29	3.51	33.4 - 40.4	2	36.92	4.96
Cloaca origin to sting	40.5 - 49.0	11	43.92	2.76	39.3 - 46.5	2	42.87	5.06
Tail width, base of sting	2.3 - 3.4	12	2.71	0.30	2.7 - 2.9	2	2.78	0.16
Tail height, base of sting	1.9 - 2.6	12	2.38	0.19	2.3 - 2.5	2	2.42	0.11
Sting length	n.a - n.a	10			n.a - n.a	2		
Snout preoral	21.2 - 30.2	14	23.24	2.31	22.7 - 23.1	3	22.90	0.23
Mouth width	6.3 - 7.3	14	6.93	0.30	7.1 - 7.8	3	7.49	0.34
Distance between nostrils	6.6 - 9.0	14	7.47	0.59	7.1 - 7.8	3	7.48	0.33
Interorbital width	12.1 - 15.1	14	13.61	0.94	13.6 - 14.3	3	13.95	0.32
Intereye width	15.9 - 24.4	14	19.50	2.19	20.0 - 20.9	3	20.33	0.50
Snout to maximum width	35.1 - 43.9	12	39.43	2.99	41.4 - 41.7	3	41.55	0.12
Eye diameter	1.9 - 5.3	14	3.73	0.87	2.8 - 3.4	3	3.20	0.32
Orbit diameter	3.1 - 7.4	14	5.30	1.11	4.9 - 5.8	3	5.43	0.44
Spiracle length	6.2 - 8.3	14	7.03	0.55	6.9 - 8.2	3	7.55	0.64
Interspiracular width	15.6 - 21.8	14	17.91	1.56	18.3 - 19.0	3	18.54	0.37
Orbit and spiracle length	7.9 - 11.5	14	9.27	1.00	9.8 - 10.2	3	9.97	0.23

...continued

Table 5.3.5b. continued.

Nostril length	3.6 - 4.7	14	4.10	0.38	4.0 - 4.4	3	4.18	0.20
Snout prenasal	16.0 - 23.3	14	17.68	1.86	16.9 - 18.0	3	17.46	0.52
Nasal curtain width	8.7 - 10.4	14	9.51	0.53	10.0 - 10.2	3	10.11	0.13
Nasal curtain length	4.3 - 6.7	12	5.28	0.65	5.6 - 6.1	3	5.85	0.22
End of orbit to pectoral insertion	58.6 - 66.8	13	61.08	1.98	60.3 - 63.4	3	62.03	1.62
Snout to origin of cloaca	77.0 - 83.6	13	79.75	2.01	79.8 - 82.7	3	81.55	1.52
Width, 1st gill slit	2.7 - 3.4	14	3.13	0.22	3.4 - 3.6	3	3.51	0.13
Width, 3rd gill slit	2.9 - 3.8	14	3.44	0.25	3.7 - 4.1	3	3.83	0.20
Width, 5th gill slit	1.6 - 2.6	14	2.15	0.27	2.5 - 2.6	3	2.54	0.06
Head length	42.5 - 51.9	14	46.13	2.45	45.7 - 47.4	3	46.72	0.93
Distance between 1st gill slits	18.0 - 22.4	13	20.28	1.04	21.0 - 22.2	3	21.76	0.68
Distance between 5th gill slits	11.1 - 14.1	13	12.95	0.76	13.5 - 13.7	3	13.63	0.07
Cloaca length	4.3 - 6.9	14	5.52	0.85	5.4 - 6.2	3	5.83	0.40
Clasper, postcloaca length	9.7 - 20.5	7	13.25	4.22	x - x	3		
Clasper, length from pelvic axil	6.2 - 16.1	7	8.88	4.04	x - x	3		

Table 5.3.6b. Counts and meristic values for *H. pastinacoides*.

	(E)		(F)	
	Range	N	Range	N
Oral papillae (floor)	n.a - n.a	14	n.a - n.a	3
Palate ridges	n.a - n.a	14	n.a - n.a	3
Upper tooth rows	n.a - n.a	14	n.a - n.a	3
Lower tooth rows	n.a - n.a	14	n.a - n.a	3
Total pectoral radials	129 - 136	9	n.a - n.a	3
Propterygial radials	50 - 53	9	n.a - n.a	3
Mesopterygial radials	18 - 22	9	n.a - n.a	3
Metapterygial radials	57 - 65	9	n.a - n.a	3
Total pelvic radials	24 - 30	9	n.a - n.a	3
Total vertebral segments	108 - 112	8	n.a - n.a	3
Monospondylous vertebrae	43 - 56	9	n.a - n.a	3
Prespine diplospondylous	63 - 69	8	n.a - n.a	3
Postspine diplospondylous	0 - 0	9	n.a - n.a	3

Table 5.3.7a. Measurements in % of disc width, for *H. uarnacoides* (Bleeker 1852). (A) BMNH 1867.11.28.210 (possible syntype, female); (B) RMNH 2467 (possible syntype, immature male); (C) BMNH 1892.6.17.15 (possible syntype of *T. bleekeri*, female); (D) CSIRO H4426.25, CSIRO H4426.26 (nontype, females, Indonesia). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)*	(C)*	(D)			
				Range	N	Mean	S.D.
Disc width (mm)	253.9	236.2	195.2	225.0 - 448.0	2	336.50	157.68
Total length	n.a	n.a	473.4	476.9 - 476.9	1	476.89	
Disc length	100.3	101.8	108.1	100.4 - 101.3	2	100.89	0.63
Snout to pectoral insert	88.3	n.a	99.1	88.2 - 91.2	2	89.68	2.12
Disc thickness	9.2	n.a	n.a	11.6 - 12.1	2	11.80	0.35
Snout preorbital	26.8	30.1	31.1	27.0 - 27.2	2	27.07	0.13
Snout preorbital (horizontal)	24.8	n.a	29.1	25.7 - 25.8	2	25.74	0.12
Length pelvic-fin	n.a	n.a	n.a	17.9 - 19.7	2	18.79	1.23
Width across pelvic-fin base	n.a	n.a	n.a	11.0 - 14.4	2	12.70	2.34
Greatest width across pelvic-fins	n.a	n.a	n.a	29.1 - 31.2	2	30.17	1.45
Cloaca origin to tail tip	n.a	n.a	n.a	390.3 - 390.3	1	390.35	
Tail width, axil of pelvics	6.1	n.a	n.a	7.0 - 7.8	2	7.39	0.61
Tail height, axil of pelvics	4.7	n.a	n.a	4.4 - 4.8	2	4.57	0.30
Pectoral insertion to sting origin	n.a	n.a	41.6	35.4 - 35.4	1	35.44	
Cloaca origin to sting	n.a	n.a	n.a	38.4 - 38.4	1	38.39	
Tail width, base of sting	n.a	n.a	n.a	3.3 - 3.3	1	3.29	
Tail height, base of sting	n.a	n.a	n.a	2.8 - 2.8	1	2.79	
Sting length	n.a	n.a	n.a	n.a - n.a	2		
Snout preoral	27.0	n.a	31.9	28.3 - 29.3	2	28.79	0.67
Mouth width	7.4	n.a	9.9	7.3 - 8.0	2	7.66	0.53
Distance between nostrils	10.2	n.a	10.3	9.7 - 10.4	2	10.02	0.51
Interorbital width	14.5	n.a	15.7	13.7 - 14.5	2	14.10	0.50
Intereye width	17.7	n.a	20.3	16.0 - 20.4	2	18.20	3.08
Snout to maximum width	44.6	n.a	47.5	44.8 - 46.3	2	45.52	1.05
Eye diameter	3.6	n.a	3.7	2.6 - 3.7	2	3.13	0.75
Orbit diameter	5.1	n.a	4.9	3.8 - 6.1	2	4.94	1.63
Spiracle length	7.1	n.a	8.0	6.0 - 7.5	2	6.78	1.06
Interspiracular width	19.6	n.a	22.3	16.2 - 21.0	2	18.61	3.35
Orbit and spiracle length	10.2	n.a	11.4	8.4 - 11.3	2	9.86	2.07

...*continued*

Table 5.3.7a. continued.

Nostril length	3.8	n.a	5.7	4.3 - 5.0	2	4.67	0.52
Snout prenasal	22.1	n.a	25.6	23.7 - 23.7	2	23.68	0.03
Nasal curtain width	10.2	n.a	11.7	10.8 - 11.2	2	11.01	0.30
Nasal curtain length	5.4	n.a	5.9	5.9 - 7.0	2	6.45	0.75
End of orbit to pectoral insertion	59.2	n.a	64.3	58.3 - 60.9	2	59.59	1.80
Snout to origin of cloaca	n.a	n.a	n.a	81.6 - 86.5	2	84.06	3.51
Width, 1st gill slit	2.1	n.a	n.a	3.1 - 3.2	2	3.14	0.04
Width, 3rd gill slit	2.4	n.a	n.a	2.1 - 3.4	2	2.75	0.88
Width, 5th gill slit	2.1	n.a	n.a	2.1 - 3.1	2	2.61	0.71
Head length	50.7	n.a	56.3	50.6 - 52.6	2	51.62	1.44
Distance between 1st gill slits	21.4	n.a	23.9	19.3 - 20.7	2	20.00	0.99
Distance between 5th gill slits	13.1	n.a	n.a	13.0 - 13.3	2	13.14	0.22
Cloaca length	n.a	n.a	n.a	4.8 - 5.8	2	5.30	0.71
Clasper, postcloaca length	x	n.a	x	x - x	2		
Clasper, length from pelvic axil	x	n.a	x	x - x	2		

Table 5.3.8a. Counts and meristic values for *H. uarnacoides*. (*counts by P. Last).

	(A)*	(B)*	(C)*	(D)	
				Range	N
Oral papillae (floor)	2	n.a	2	2 - 2	1
Palate ridges	n.a	n.a	n.a	n.a - n.a	2
Upper tooth rows	n.a	n.a	n.a	n.a - n.a	2
Lower tooth rows	n.a	n.a	n.a	n.a - n.a	2
Total pectoral radials	n.a	n.a	n.a	143 - 144	1
Propterygial radials	n.a	n.a	n.a	52 - 56	1
Mesopterygial radials	n.a	n.a	n.a	27 - 30	1
Metapterygial radials	n.a	n.a	n.a	61 - 61	1
Total pelvic radials	n.a	n.a	n.a	27 - 28	1
Total vertebral segments	n.a	n.a	n.a	109 - 109	1
Monospondylous vertebrae	n.a	n.a	n.a	49 - 49	1
Prespine diplospondylous	n.a	n.a	n.a	60 - 60	1
Postspine diplospondylous	n.a	n.a	n.a	0 - 0	1

Table 5.3.7b. Measurements in % of disc width, for *H. uarnacoides* (Bleeker 1852). (E) CSIRO H5472.03 (nontype, immature male, Kuching, Sarawak); (F) CSIRO H5470.01 (nontype, mature male, Kota Kinabalu, Sabah); (G) CSIRO H4921.01, CSIRO H4921.02, CSIRO H4921.03, CSIRO H5479.17, CSIRO H5479.18, CSIRO H5479.19, CSIRO H5481.03, CSIRO H5616.01, CSIRO H5616.02, CSIRO H5616.03, CSIRO H5616.04, CSIRO H5616.05, CSIRO H5616.06, SMKK KTG112698, UMS MMSK45, UMS MMSK46, UMS MMSK53 (nontype, males and females, Sandakan, Sabah). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(E)	(F)	(G)			
			Range	N	Mean	S.D.
Disc width (mm)	305.0	810.0	200.0 - 427.0	17	288.29	71.83
Total length	473.1	n.a	393.8 - 494.5	13	439.41	34.03
Disc length	102.3	99.4	99.4 - 105.2	17	101.81	2.04
Snout to pectoral insert	92.1	n.a	87.9 - 94.1	17	90.88	2.00
Disc thickness	11.5	12.3	9.4 - 14.1	17	12.09	1.21
Snout preorbital	30.1	n.a	26.5 - 29.1	17	27.88	0.76
Snout preorbital (horizontal)	29.3	n.a	24.4 - 27.9	17	26.28	0.93
Length pelvic-fin	19.6	18.0	17.2 - 21.5	16	19.53	1.17
Width across pelvic-fin base	12.7	11.2	9.8 - 14.2	17	12.87	1.12
Greatest width across pelvic-fins	28.9	37.9	25.0 - 29.8	4	26.85	2.07
Cloaca origin to tail tip	387.2	n.a	309.9 - 408.5	13	354.17	32.60
Tail width, axil of pelvics	6.8	5.9	5.9 - 9.1	17	7.23	0.84
Tail height, axil of pelvics	4.6	4.4	3.7 - 5.8	17	4.68	0.60
Pectoral insertion to sting origin	37.0	n.a	26.2 - 41.5	15	36.09	3.82
Cloaca origin to sting	39.0	n.a	32.7 - 46.8	15	40.87	3.38
Tail width, base of sting	2.5	n.a	2.3 - 3.3	15	2.70	0.28
Tail height, base of sting	2.4	n.a	2.3 - 3.3	15	2.65	0.27
Sting length	n.a	n.a	15.9 - 15.9	1	15.88	
Snout preoral	30.9	n.a	27.4 - 30.8	17	28.86	0.82
Mouth width	7.4	7.2	6.9 - 8.3	17	7.61	0.48
Distance between nostrils	9.8	8.8	8.9 - 10.6	17	9.76	0.39
Interorbital width	13.2	13.5	12.8 - 16.6	17	13.85	0.88
Intereye width	17.4	16.4	16.7 - 23.0	17	18.88	1.53
Snout to maximum width	45.1	n.a	42.7 - 48.6	17	45.72	1.85
Eye diameter	2.8	2.2	2.5 - 4.2	17	3.53	0.52
Orbit diameter	5.2	5.3	4.1 - 6.2	17	5.43	0.76
Spiracle length	6.7	5.9	6.1 - 8.2	17	6.74	0.53
Interspiracular width	17.8	16.3	17.1 - 22.1	17	18.78	1.42
Orbit and spiracle length	9.4	8.8	8.8 - 11.1	17	9.88	0.66

...continued

Table 5.3.7b. continued.

Nostril length	4.8	4.1	4.2 - 5.1	17	4.69	0.24
Snout prenasal	24.6	n.a	21.8 - 24.6	17	23.00	0.67
Nasal curtain width	10.9	10.6	10.0 - 11.3	17	10.73	0.42
Nasal curtain length	5.7	6.0	4.9 - 6.9	17	5.88	0.54
End of orbit to pectoral insertion	58.0	59.3	56.5 - 63.2	17	59.72	1.66
Snout to origin of cloaca	85.9	n.a	82.3 - 88.7	17	85.21	2.08
Width, 1st gill slit	3.1	3.0	2.6 - 3.3	17	2.91	0.18
Width, 3rd gill slit	3.1	3.1	2.7 - 3.3	17	3.18	0.17
Width, 5th gill slit	1.9	2.2	1.8 - 2.3	17	2.07	0.19
Head length	52.7	n.a	50.2 - 55.0	17	51.99	1.34
Distance between 1st gill slits	20.1	18.5	18.8 - 21.2	17	19.96	0.64
Distance between 5th gill slits	12.4	12.1	12.4 - 13.7	17	13.04	0.48
Cloaca length	4.8	4.1	4.3 - 6.1	17	5.09	0.44
Clasper, postcloaca length	9.8	18.1	8.7 - 11.1	8	9.84	0.72
Clasper, length from pelvic axil	5.1	13.0	6.1 - 7.6	8	6.79	0.53

Table 5.3.8b. Counts and meristic values for *H. uarnacoides*.

	(E)	(F)	(G)	
			Range	N
Oral papillae (floor)	n.a	2	2 - 2	8
Palate ridges	n.a	n.a	n.a - n.a	8
Upper tooth rows	n.a	n.a	n.a - n.a	8
Lower tooth rows	n.a	n.a	n.a - n.a	8
Total pectoral radials	145	n.a	141 - 147	5
Propterygial radials	58-59	n.a	56 - 59	5
Mesopterygial radials	23	n.a	23 - 28	5
Metapterygial radials	63-64	n.a	58 - 63	5
Total pelvic radials	23-25	n.a	25 - 29	4
Total vertebral segments	107	n.a	104 - 111	5
Monospondylous vertebrae	46	n.a	49 - 55	5
Prespine diplospondylous	61	n.a	51 - 62	5
Postspine diplospondylous	0	n.a	0 - 0	5

Table 5.3.7c. Measurements in % of disc width, for *H. uarnacoides* (Bleeker 1852). (H) MTUF 30000 (nontype, female, India); (I) CAS 213287(1of2), CAS 213287(2of2), CAS 213289 (nontype, females and a male, Thailand). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(H)	(I)			
		Range	N	Mean	S.D.
Disc width (mm)	311.0	247.0 - 290.0	3	264.33	22.68
Total length	420.9	437.2 - 470.0	2	453.64	23.19
Disc length	103.2	102.0 - 102.8	3	102.29	0.48
Snout to pectoral insert	91.1	90.7 - 93.3	3	91.82	1.35
Disc thickness	12.6	10.3 - 12.8	3	11.96	1.40
Snout preorbital	29.4	25.7 - 29.1	3	27.60	1.73
Snout preorbital (horizontal)	28.5	25.0 - 27.9	3	26.43	1.43
Length pelvic-fin	18.7	19.3 - 19.9	3	19.53	0.33
Width across pelvic-fin base	13.0	12.3 - 13.8	3	13.04	0.71
Greatest width across pelvic-fins	30.5	27.0 - 30.1	3	28.29	1.64
Cloaca origin to tail tip	335.0	350.9 - 380.4	2	365.63	20.89
Tail width, axil of pelvics	6.6	6.6 - 8.4	3	7.54	0.89
Tail height, axil of pelvics	4.9	4.9 - 5.4	3	5.14	0.29
Pectoral insertion to sting origin	36.8	30.6 - 36.3	3	34.08	3.04
Cloaca origin to sting	40.1	36.3 - 39.3	3	38.10	1.61
Tail width, base of sting	2.5	2.7 - 3.0	3	2.85	0.13
Tail height, base of sting	2.5	2.6 - 2.8	3	2.74	0.10
Sting length	n.a	14.9 - 14.9	1	14.89	
Snout preoral	30.4	27.8 - 29.5	3	28.79	0.88
Mouth width	6.5	7.5 - 8.1	3	7.87	0.32
Distance between nostrils	9.2	9.3 - 10.1	3	9.80	0.45
Interorbital width	12.7	14.0 - 15.6	3	14.83	0.81
Intereye width	17.1	19.9 - 20.9	3	20.58	0.56
Snout to maximum width	40.9	44.5 - 49.7	3	46.52	2.81
Eye diameter	3.2	3.5 - 4.0	3	3.79	0.27
Orbit diameter	4.8	4.6 - 6.6	3	5.36	1.10
Spiracle length	5.5	6.5 - 7.5	3	6.93	0.53
Interspiracular width	17.5	19.7 - 22.1	3	20.77	1.22
Orbit and spiracle length	9.2	9.1 - 12.4	3	10.33	1.85

...continued

Table 5.3.7c. continued.

Nostril length	4.7	4.1 - 4.7	3	4.46	0.30
Snout prenasal	24.8	22.3 - 23.0	3	22.63	0.36
Nasal curtain width	9.9	10.6 - 11.4	3	11.01	0.41
Nasal curtain length	5.5	5.7 - 6.4	3	6.10	0.36
End of orbit to pectoral insertion	58.2	59.4 - 62.9	3	61.07	1.76
Snout to origin of cloaca	85.9	86.3 - 89.6	3	87.43	1.92
Width, 1st gill slit	2.6	2.8 - 3.0	3	2.87	0.13
Width, 3rd gill slit	2.8	3.1 - 3.5	3	3.27	0.19
Width, 5th gill slit	2.1	2.0 - 2.3	3	2.13	0.16
Head length	52.1	51.8 - 53.4	3	52.61	0.82
Distance between 1st gill slits	18.8	21.2 - 22.6	3	21.84	0.68
Distance between 5th gill slits	12.3	13.7 - 14.5	3	14.14	0.40
Cloaca length	3.4	2.9 - 4.3	3	3.53	0.72
Clasper, postcloaca length	x	11.9 - 11.9	1	11.95	
Clasper, length from pelvic axil	x	6.9 - 6.9	1	6.88	

Table 5.3.8c. Counts and meristic values for *H. uarnacoides*.

	(H)	(I)	
		Range	N
Oral papillae (floor)	n.a	2 - 2	2
Palate ridges	n.a	n.a - n.a	2
Upper tooth rows	n.a	n.a - n.a	2
Lower tooth rows	n.a	n.a - n.a	2
Total pectoral radials	144-146	n.a - n.a	3
Propterygial radials	56-57	n.a - n.a	3
Mesopterygial radials	26	n.a - n.a	3
Metapterygial radials	61-64	n.a - n.a	3
Total pelvic radials	27	n.a - n.a	3
Total vertebral segments	110	n.a - n.a	3
Monospondylous vertebrae	55	n.a - n.a	3
Prespine diplospondylous	55	n.a - n.a	3
Postspine diplospondylous	0	n.a - n.a	3

Table 5.3.9. Measurements in % of disc width, for *H.* sp. E. (A) CSIRO H5155.0 (single largest mature male); (B) CSIRO H5285.01, CSIRO H4915.01, CSIRO H4917.01, CSIRO H4916.01, CSIRO H4549.02. N is number of specimens from which means and standard deviations (S.D.) were taken.

	(A)	(B)			
		Range	N	Mean	S.D.
Disc width (mm)	707.0	246.0 - 430.0	5	310.60	73.03
Total length	338.9	377.7 - 404.1	2	390.87	18.66
Disc length	108.2	108.9 - 111.9	5	110.37	1.24
Snout to pectoral insert	99.0	98.0 - 100.5	5	99.29	1.09
Disc thickness	11.3	8.0 - 11.5	5	9.69	1.57
Snout preorbital	39.3	37.6 - 39.4	5	38.32	0.88
Snout preorbital (horizontal)	38.0	36.4 - 38.3	5	37.24	0.84
Length pelvic-fin	19.4	17.1 - 21.4	5	19.82	1.79
Width across pelvic-fin base	11.5	11.0 - 12.0	5	11.40	0.39
Greatest width across pelvic-fins	n.a	34.3 - 40.5	2	37.39	4.36
Cloaca origin to tail tip	246.5	289.1 - 312.7	2	300.89	16.66
Tail width, axil of pelvics	5.7	5.2 - 7.2	5	6.41	0.73
Tail height, axil of pelvics	4.1	4.3 - 4.8	5	4.52	0.19
Pectoral insertion to sting origin	33.0	32.4 - 35.1	5	34.13	1.11
Cloaca origin to sting	39.2	39.2 - 41.1	5	40.42	0.80
Tail width, base of sting	2.2	2.0 - 2.8	5	2.37	0.32
Tail height, base of sting	2.0	2.3 - 2.6	5	2.43	0.13
Sting 1 length	n.a	17.0 - 19.4	2	18.22	1.70
Sting 2 length	x	3.7 - 3.7	1	3.67	
Snout preoral	38.7	37.1 - 38.4	5	37.89	0.51
Mouth width	7.7	7.6 - 8.0	5	7.79	0.18
Distance between nostrils	10.9	10.2 - 11.3	5	10.86	0.45
Interorbital width	13.8	13.0 - 14.9	5	13.74	0.77
Intereye width	15.8	15.5 - 19.0	5	16.90	1.38
Snout to maximum width	51.7	51.7 - 57.9	5	54.61	2.44
Eye diameter	1.2	1.5 - 2.0	5	1.80	0.20
Orbit diameter	2.2	3.0 - 3.4	5	3.23	0.21
Spiracle length	5.5	6.4 - 7.2	5	6.77	0.30
Interspiracular width	16.7	16.1 - 18.6	5	17.14	1.27
Orbit and spiracle length	7.2	8.4 - 9.4	5	9.03	0.42

...continued

Table 5.3.9. continued.

Nostril length	3.7	3.6 - 6.6	5	4.37	1.29
Snout prenasal	32.0	31.5 - 33.4	5	32.30	0.80
Nasal curtain width	6.9	6.0 - 6.7	5	6.38	0.30
Nasal curtain length	12.1	11.1 - 12.2	5	11.62	0.40
End of orbit to pectoral insertion	57.3	56.7 - 61.8	5	59.29	1.81
Snout to origin of cloaca	92.4	88.6 - 93.3	5	91.80	1.96
Width, 1st gill slit	3.3	2.6 - 3.4	5	3.00	0.33
Width, 3rd gill slit	3.5	2.7 - 3.9	5	3.29	0.43
Width, 5th gill slit	2.0	1.5 - 2.4	5	1.95	0.39
Head length	60.3	60.1 - 61.3	5	60.60	0.43
Distance between 1st gill slits	19.2	17.8 - 19.7	5	18.77	0.81
Distance between 5th gill slits	14.1	13.0 - 14.6	5	13.62	0.61
Cloaca length	4.3	3.8 - 5.4	5	4.74	0.61
Clasper, postcloaca length	17.1	10.3 - 10.4	2	10.38	0.07
Clasper, length from pelvic axil	13.0	4.6 - 6.5	2	5.53	1.30

Table 5.3.10. Counts and meristic values for *H.* sp. E.

	(A)	(B)	
		Range	N
Oral papillae (floor)	0	0 - 0	4
Palate ridges	1	1 - 1	3
Upper tooth rows	25	21 - 22	3
Lower tooth rows	28	24 - 27	3
Total pectoral radials	136-138	139 - 144	5
Propterygial radials	55-57	55 - 59	5
Mesopterygial radials	27-30	29 - 31	4
Metapterygial radials	51-54	53 - 57	4
Total pelvic radials	23	20 - 27	5
Total vertebral segments	100	99 - 102	5
Monospondylous vertebrae	46	41 - 47	4
Prespine diplospondylous	54	53 - 59	4
Postspine diplospondylous	0	0 - 0	5

Table 5.3.11. Measurements in % of disc width, for *H.* sp. F.

	CSIRO H5485.01	CSIRO H5472.01
Disc width (mm)	515.9	343.0
Total length	n.a	n.a
Disc length	113.5	111.7
Snout to pectoral insert	101.5	99.7
Disc thickness	12.6	11.4
Snout preorbital	38.5	35.7
Snout preorbital (horizontal)	37.9	35.0
Length pelvic fin	23.3	24.0
Width across pelvic-fin base	13.9	16.4
Greatest width across pelvic-fins	46.1	35.6
Cloaca origin to tail tip	n.a	n.a
Tail width, axil of pelvics	7.9	8.0
Tail height, axil of pelvics	4.5	4.8
Pectoral insertion to sting origin	n.a	n.a
Cloaca origin to sting	n.a	n.a
Tail width, base of sting	n.a	n.a
Tail height, base of sting	n.a	n.a
Sting length	n.a	n.a
Snout preoral	37.1	35.5
Mouth width	8.5	8.2
Distance between nostrils	8.7	9.5
Interorbital width	14.5	13.5
Intereye width	15.7	15.1
Snout to maximum width	56.8	52.2
Eye diameter	1.3	1.7
Orbit diameter	2.3	3.2
Spiracle length	7.4	7.8
Interspiracular width	16.1	16.5
Orbit and spiracle length	8.7	9.7

...continued

Table 5.3.11. continued.

Nostril length	3.3	3.9
Snout prenasal	31.2	28.8
Nasal curtain width	10.7	10.4
Nasal curtain length	5.7	5.6
End of orbit to pectoral insertion	61.5	61.2
Snout to origin of cloaca	93.8	91.5
Width, 1st gill slit	3.5	3.4
Width, 3rd gill slit	3.7	3.7
Width, 5th gill slit	2.7	2.5
Head length	61.3	59.9
Distance between 1st gill slits	20.6	21.7
Distance between 5th gill slits	15.8	15.6
Cloaca length	5.1	8.0
Clasper, postcloaca length	x	x
Clasper, length from pelvic axil	x	x

Table 5.3.12. Counts and meristic values for *H.* sp. F.

	CSIRO H5485.01	CSIRO H5472.01
Oral papillae (floor)	none	none
Palate ridges	3	3
Upper tooth rows	34	29
Lower tooth rows	36	31
Total pectoral radials	144	144
Propterygial radials	64-65	63
Mesopterygial radials	20-21	22
Metapterygial radials	59	59
Total pelvic radials	26-27	28-29
Total vertebral segments	n.a	n.a
Monospondylous vertebrae	45	46
Prespine diplospondylous	n.a	41+
Postspine diplospondylous	0?	0?

Table 5.4.1a. Measurements in % of disc width, for *H. imbricata* (Bloch & Schneider 1801). (A) ZMB 7585 (holotype, mature male); (B) RMNH 7446 (possible holotype of *T. dadong*, female); (C) CAS 141045 (nontype, immature male, mouth Ganges River); (D) NTM S13160.009 (nontype, female; Chilaw, Sri Lanka); (E) BPBM 33199(1of2) (nontype, immature male; Kuwait); (F) BPBM 33199(2of2) (nontype, female; Kuwait); (G) LACM 38129-83(2of3), LACM 38130-60(3of10), LACM 38134-37(1of2) (nontype, females; Sind, Pakistan). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)*	(C)	(D)	(E)	(F)	(G)			
							Range	N	Mean	S.D.
Disc width (mm)	125.0	164.0	145.0	188.0	103.0	190.0	176.0 - 207.0	3	186.33	17.90
Total length	248.0	199.4	229.7	195.7	220.4	187.9	202.8 - 215.5	2	209.15	8.92
Disc length	120.0	104.3	105.5	111.4	102.1	106.8	101.7 - 105.3	3	103.29	1.85
Snout to pectoral insert	n.a	n.a	97.6	99.6	93.1	98.8	92.5 - 94.8	3	93.61	1.17
Disc thickness	n.a	n.a	11.2	10.4	9.9	10.7	11.9 - 12.9	3	12.35	0.47
Snout preorbital	n.a	29.9	31.9	32.1	31.0	31.4	28.6 - 30.3	3	29.40	0.86
Snout preorbital (horizontal)	n.a	n.a	30.9	31.1	31.6	30.2	28.1 - 29.2	3	28.52	0.61
Length pelvic-fin	n.a	22.0	19.8	21.9	20.4	20.2	20.1 - 21.9	3	21.14	0.95
Width across pelvic-fin base	n.a	n.a	14.1	16.2	12.8	15.4	13.6 - 16.3	3	14.74	1.37
Greatest width across pelvic-fins	n.a	24.4	40.3	35.0	35.0	34.5	36.6 - 41.1	3	38.47	2.37
Cloaca origin to tail tip	n.a	104.3	136.8	102.8	133.8	96.9	116.1 - 128.1	2	122.11	8.50
Tail width, axil of pelvics	n.a	9.6	10.6	8.5	8.0	9.6	10.4 - 10.6	3	10.46	0.09
Tail height, axil of pelvics	n.a	5.4	5.9	5.3	5.5	6.4	6.1 - 7.1	3	6.75	0.56
Pectoral insertion to sting origin	n.a	n.a	34.1	23.5	26.0	29.3	29.7 - 31.3	3	30.57	0.83
Cloaca origin to sting	n.a	26.2	37.0	30.2	31.9	35.2	34.5 - 36.3	3	35.51	0.88
Tail width, base of sting	n.a	n.a	5.0	4.5	4.3	4.5	4.4 - 5.3	3	4.80	0.46
Tail height, base of sting	n.a	n.a	4.1	3.5	3.3	3.2	3.9 - 4.1	3	4.01	0.14
Sting 1 length	n.a	25.9	27.0	n.a	29.7	17.7	14.9 - 20.3	3	18.16	2.85
Sting 2 length	n.a	34.8	39.1	n.a	n.a	n.a	22.2 - 30.8	3	27.33	4.50
Snout preoral	n.a	30.5	34.1	33.5	32.2	32.5	29.0 - 32.4	3	30.89	1.73
Mouth width	n.a	10.6	9.5	7.9	8.1	7.7	7.8 - 9.3	3	8.51	0.79
Distance between nostrils	n.a	12.0	12.3	10.2	11.0	10.4	10.5 - 12.3	3	11.50	0.91
Interorbital width	9.6	12.0	11.4	10.6	10.8	11.6	10.9 - 11.7	3	11.29	0.35
Intereye width	n.a	n.a	16.3	16.1	18.8	16.2	16.4 - 16.8	3	16.56	0.18
Snout to maximum width	n.a	42.1	47.7	49.4	42.3	48.3	45.5 - 48.2	3	47.21	1.50
Eye diameter	n.a	4.7	3.7	4.0	4.7	4.6	3.6 - 3.9	3	3.77	0.12
Orbit diameter	6.4	7.0	7.2	6.2	7.1	5.8	6.1 - 6.4	3	6.32	0.15
Spiracle length	n.a	5.1	6.1	5.5	5.0	5.2	4.8 - 5.8	3	5.37	0.54
Interspiracular width	n.a	16.5	16.3	15.6	17.0	16.1	15.5 - 16.8	3	16.31	0.68
Orbit and spiracle length	n.a	9.9	11.6	9.7	9.8	9.3	9.8 - 10.3	3	10.04	0.24

...continued

Table 5.4.1a. continued.

Nostril length	n.a	n.a	4.5	4.2	5.0	4.7	4.2 - 4.9	3	4.59	0.35
Snout prenasal	n.a	25.6	26.9	27.7	26.4	26.2	22.3 - 26.2	3	24.89	2.20
Nasal curtain width	n.a	n.a	12.1	n.a	n.a	n.a	10.9 - 12.1	3	11.30	0.66
Nasal curtain length	n.a	4.9	7.5	6.3	6.9	7.2	6.5 - 6.6	3	6.56	0.07
End of orbit to pectoral insertion	n.a	n.a	60.1	94.3	55.9	62.5	57.7 - 60.6	3	58.77	1.59
Snout to origin of cloaca	n.a	95.1	92.8	93.0	86.6	91.0	86.3 - 87.3	3	86.80	0.50
Width, 1st gill slit	n.a	2.6	2.8	3.1	3.1	3.0	3.0 - 3.2	3	3.03	0.12
Width, 3rd gill slit	n.a	2.7	2.8	3.3	2.8	3.3	3.1 - 3.6	3	3.31	0.24
Width, 5th gill slit	n.a	2.0	1.8	2.4	1.8	2.2	1.8 - 2.2	3	1.99	0.17
Head length	n.a	n.a	58.3	58.1	57.1	56.7	55.2 - 56.6	3	55.94	0.71
Distance between 1st gill slits	n.a	22.1	22.5	22.7	22.3	22.1	21.8 - 24.5	3	22.82	1.45
Distance between 5th gill slits	n.a	14.4	14.7	13.8	15.8	15.0	14.2 - 15.3	3	14.77	0.57
Cloaca length	n.a	n.a	4.6	7.1	4.4	6.5	4.8 - 5.8	3	5.30	0.50
Clasper. postcloaca length	n.a	x	14.3	x	10.5	x	x - x	3		
Clasper, length from pelvic axil	n.a	x	7.9	x	6.3	x	x - x	3		

Table 5.4.2a. Counts and meristic values for *H. imbricata*. (*count by P. Last).

	(A)	(B)*	(C)	(D)	(E)	(F)	(G)	
							Range	N
Oral papillae (floor)	n.a	2	n.a	n.a	n.a	n.a	n.a - n.a	3
Palate ridges	n.a	n.a	n.a	n.a	n.a	n.a	n.a - n.a	3
Upper tooth rows	n.a	n.a	n.a	n.a	n.a	n.a	n.a - n.a	3
Lower tooth rows	n.a	n.a	n.a	n.a	n.a	n.a	n.a - n.a	3
Total pectoral radials	n.a	n.a	n.a	107	106-108	107-108	n.a - n.a	3
Propterygial radials	n.a	n.a	n.a	46	47-48	49	n.a - n.a	3
Mesopterygial radials	n.a	n.a	n.a	16-17	13-14	13-14	n.a - n.a	3
Metapterygial radials	n.a	n.a	n.a	44-45	46	45	n.a - n.a	3
Total pelvic radials	n.a	n.a	n.a	25-26	19	25	n.a - n.a	3
Total vertebral segments	n.a	n.a	n.a	91	95	99	n.a - n.a	3
Monospondylous vertebrae	n.a	n.a	n.a	37	38	38	n.a - n.a	3
Prespine diplospondylous	n.a	n.a	n.a	43	53	51	n.a - n.a	3
Postspine diplospondylous	n.a	n.a	n.a	11	4	10	n.a - n.a	3

Table 5.4.1b. Measurements in % of disc width, for *H. imbricata* (Bloch & Schneider 1801). (H) LACM 38129-83(1of3), LACM 38129-83(3of3), LACM 38130-60(4of10) (nontype, immature males; Sind, Pakistan); (I) LACM 38130-60(1of10), LACM 38130-60(2of10), LACM 38314-24 (nontype, mature males; Sind, Pakistan). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(H)				(I)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	158.0 - 203.0	3	180.00	22.52	214.0 - 245.0	3	230.33	15.57
Total length	231.5 - 238.0	3	234.90	3.23	225.7 - 229.7	3	227.05	2.33
Disc length	102.5 - 103.4	3	102.99	0.47	102.0 - 103.3	3	102.63	0.62
Snout to pectoral insert	92.0 - 92.6	3	92.38	0.34	90.7 - 94.6	3	92.67	1.94
Disc thickness	11.4 - 12.3	3	11.79	0.47	12.3 - 13.0	3	12.76	0.38
Snout preorbital	29.8 - 30.2	3	29.96	0.17	26.7 - 30.1	3	28.03	1.81
Snout preorbital (horizontal)	28.5 - 28.8	3	28.62	0.15	25.6 - 29.0	3	26.91	1.86
Length pelvic-fin	19.9 - 20.3	3	20.03	0.23	20.3 - 21.7	2	20.97	0.98
Width across pelvic-fin base	14.0 - 14.8	3	14.30	0.41	13.0 - 14.1	2	13.57	0.77
Greatest width across pelvic-fins	36.5 - 37.5	3	36.89	0.53	33.4 - 34.2	2	33.80	0.62
Cloaca origin to tail tip	146.4 - 150.7	3	148.97	2.30	138.2 - 143.7	3	140.84	2.71
Tail width, axil of pelvics	9.5 - 10.2	3	9.89	0.38	9.0 - 12.0	3	10.13	1.65
Tail height, axil of pelvics	6.1 - 6.7	3	6.40	0.31	5.6 - 7.6	3	6.33	1.09
Pectoral insertion to sting origin	25.2 - 30.4	3	28.57	2.96	26.7 - 30.8	3	28.16	2.26
Cloaca origin to sting	30.9 - 34.9	3	33.09	1.99	30.5 - 31.4	2	30.98	0.64
Tail width, base of sting	4.7 - 5.1	3	4.94	0.23	4.6 - 5.0	3	4.76	0.22
Tail height, base of sting	3.9 - 4.3	3	4.05	0.18	3.3 - 4.0	3	3.60	0.39
Sting 1 length	18.2 - 23.2	3	19.99	2.79	10.8 - 19.9	2	15.34	6.43
Sting 2 length	20.7 - 27.8	3	24.61	3.62	13.9 - 31.4	2	22.68	12.38
Sting 3 length	x - x	3			27.0 - 27.0	1	27.00	
Snout preoral	30.6 - 31.0	3	30.81	0.20	27.7 - 31.4	3	29.12	1.96
Mouth width	8.1 - 8.8	3	8.32	0.38	8.2 - 8.6	3	8.37	0.19
Distance between nostrils	11.3 - 11.6	3	11.42	0.13	11.6 - 12.3	3	11.98	0.37
Interorbital width	11.1 - 12.1	3	11.55	0.54	11.9 - 12.4	3	12.09	0.27
Intereye width	15.8 - 17.9	3	16.87	1.07	15.9 - 17.2	3	16.35	0.74
Snout to maximum width	46.0 - 47.2	3	46.44	0.63	45.0 - 50.5	3	47.05	3.02
Eye diameter	3.7 - 4.1	3	3.89	0.19	3.3 - 3.9	3	3.62	0.30
Orbit diameter	6.0 - 6.1	3	6.03	0.03	6.1 - 7.7	3	6.88	0.83
Spiracle length	4.9 - 5.8	3	5.50	0.49	5.2 - 6.1	3	5.57	0.50
Interspiracular width	15.8 - 16.7	3	16.40	0.50	16.3 - 16.8	3	16.59	0.26
Orbit and spiracle length	9.4 - 10.2	3	9.88	0.40	10.2 - 11.3	3	10.64	0.56

...continued

Table 5.4.1b. continued.

Nostril length	3.9 - 4.6	3	4.31	0.35	4.1 - 4.3	3	4.21	0.10
Snout prenasal	25.2 - 25.7	3	25.51	0.26	22.3 - 24.9	3	23.42	1.37
Nasal curtain width	11.4 - 11.8	3	11.62	0.23	13.3 - 13.7	3	13.50	0.17
Nasal curtain length	6.2 - 6.7	3	6.42	0.24	6.8 - 7.1	3	6.89	0.14
End of orbit to pectoral insertion	57.3 - 58.4	3	58.06	0.62	57.8 - 60.4	3	58.96	1.31
Snout to origin of cloaca	85.2 - 87.2	3	85.93	1.13	85.1 - 87.5	3	86.21	1.20
Width, 1st gill slit	2.7 - 2.9	3	2.79	0.11	2.7 - 3.5	3	2.98	0.46
Width, 3rd gill slit	2.9 - 3.4	3	3.11	0.22	3.0 - 3.6	3	3.29	0.28
Width, 5th gill slit	1.8 - 1.9	3	1.85	0.06	2.2 - 20.7	3	8.35	10.69
Head length	54.8 - 55.8	3	55.23	0.52	54.7 - 57.1	3	55.70	1.25
Distance between 1st gill slits	20.4 - 22.5	3	21.65	1.09	21.9 - 24.2	3	23.44	1.30
Distance between 5th gill slits	14.6 - 15.1	3	14.85	0.24	13.8 - 14.9	3	14.48	0.59
Cloaca length	4.2 - 4.8	3	4.58	0.30	4.1 - 5.2	3	4.60	0.58
Clasper, postcloaca length	13.7 - 18.7	3	15.62	2.74	16.1 - 17.0	2	16.53	0.62
Clasper, length from pelvic axil	8.9 - 13.7	3	10.59	2.69	12.0 - 13.1	2	12.54	0.78

Table 5.4.2b. Counts and meristic values for *H. imbricata*.

	(H)		(I)	
	Range	N	Range	N
Oral papillae (floor)	n.a - n.a	3	n.a - n.a	3
Palate ridges	n.a - n.a	3	n.a - n.a	3
Upper tooth rows	n.a - n.a	3	n.a - n.a	3
Lower tooth rows	n.a - n.a	3	n.a - n.a	3
Total pectoral radials	n.a - n.a	3	n.a - n.a	3
Propterygial radials	n.a - n.a	3	n.a - n.a	3
Mesopterygial radials	n.a - n.a	3	n.a - n.a	3
Metapterygial radials	n.a - n.a	3	n.a - n.a	3
Total pelvic radials	n.a - n.a	3	n.a - n.a	3
Total vertebral segments	n.a - n.a	3	n.a - n.a	3
Monospondylous vertebrae	n.a - n.a	3	n.a - n.a	3
Prespine diplospondylous	n.a - n.a	3	n.a - n.a	3
Postspine diplospondylous	n.a - n.a	3	n.a - n.a	3

Table 5.4.3a. Measurements in % of disc width, for *H. oxyrhyncha* (Sauvage 1878). (A) MNHN 9639 (holotype, female); (B) MNHN 1922-79 (one of three syntypes of *H. krempfi*, female); (C) MNHN 1922-77, MNHN 1922-78 (two of three syntypes of *H. krempfi*, males). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)*	(C)*			
			Range	N	Mean	S.D.
Disc width (mm)	242.8	117.2	88.5 - 135.4	2	111.94	33.12
Total length	444.0	459.1	395.4 - 472.8	2	434.10	54.75
Disc length	117.3	118.3	114.9 - 115.3	2	115.09	0.32
Snout to pectoral insert	102.5	105.8	102.6 - 103.4	2	102.96	0.56
Disc thickness	7.8	10.4	11.7 - 13.1	2	12.43	0.96
Snout preorbital	36.3	35.7	30.9 - 35.0	2	32.95	2.89
Snout preorbital (horizontal)	35.0	34.5	28.6 - 34.3	2	31.45	3.99
Length pelvic-fin	24.1	23.7	25.3 - 26.7	2	26.03	0.98
Width across pelvic-fin base	15.8	14.8	15.1 - 15.3	2	15.22	0.13
Greatest width across pelvic-fins	n.a	45.9	33.9 - 36.9	2	35.43	2.11
Cloaca origin to tail tip	344.8	357.7	295.7 - 377.3	2	336.48	57.74
Tail width, axil of pelvics	9.0	10.1	9.3 - 10.3	2	9.80	0.64
Tail height, axil of pelvics	7.0	6.6	6.7 - 7.7	2	7.19	0.71
Pectoral insertion to sting origin	47.5	49.8	46.2 - 50.7	2	48.47	3.21
Cloaca origin to sting	53.6	55.5	48.3 - 50.4	2	49.36	1.45
Tail width, base of sting	3.5	4.7	5.1 - 5.3	2	5.20	0.09
Tail height, base of sting	3.4	4.2	4.3 - 4.8	2	4.55	0.40
Sting length	n.a	n.a	n.a - n.a	2		
Snout preoral	35.9	36.1	33.4 - 36.1	2	34.73	1.93
Mouth width	9.1	9.3	9.3 - 10.4	2	9.87	0.80
Distance between nostrils	10.0	10.4	10.9 - 11.5	2	11.18	0.43
Interorbital width	14.0	13.4	13.7 - 13.8	2	13.72	0.10
Intereye width	16.0	19.3	18.6 - 20.2	2	19.41	1.07
Snout to maximum width	54.9	55.2	51.0 - 53.3	2	52.15	1.69
Eye diameter	3.0	4.0	3.6 - 4.3	2	3.93	0.46
Orbit diameter	4.4	6.5	6.3 - 6.3	2	6.28	0.04
Spiracle length	6.8	6.3	6.3 - 8.1	2	7.19	1.30
Interspiracular width	16.8	20.2	18.9 - 21.4	2	20.12	1.74
Orbit and spiracle length	9.8	10.0	10.8 - 11.6	2	11.20	0.58

...*continued*

Table 5.4.3a. continued.

Nostril length	4.3	5.1	4.9 - 5.2	2	5.07	0.18
Snout prenasal	30.5	28.6	25.6 - 29.8	2	27.72	2.99
Nasal curtain width	10.0	11.1	12.4 - 13.0	2	12.71	0.46
Nasal curtain length	4.4	6.7	6.5 - 6.7	2	6.59	0.11
End of orbit to pectoral insertion	64.2	65.8	62.8 - 66.1	2	64.49	2.34
Snout to origin of cloaca	99.2	101.4	95.5 - 99.7	2	97.62	2.99
Width, 1st gill slit	2.8	2.7	2.8 - 2.8	2	2.78	0.00
Width, 3rd gill slit	3.6	3.6	3.3 - 3.8	2	3.58	0.33
Width, 5th gill slit	2.6	2.2	2.1 - 2.7	2	2.39	0.40
Head length	62.0	63.5	62.7 - 62.9	2	62.83	0.16
Distance between 1st gill slits	22.6	24.2	23.6 - 24.0	2	23.79	0.27
Distance between 5th gill slits	n.a	16.6	16.5 - 17.3	2	16.94	0.57
Cloaca length	5.0	4.2	4.2 - 5.2	2	4.68	0.70
Clasper, postcloaca length	x	x	11.3 - 12.5	2	11.88	0.89
Clasper, length from pelvic axil	x	x	2.0 - 4.3	2	3.15	1.66

Table 5.4.4a. Counts and meristic values for *H. oxyrhyncha*. (*counts by P. Last; ‡data given in Deynat & Fermon 2001).

	(A)	(B)	(C)	
			Range	N
Oral papillae (floor)	5*	4*	4 - 4*	2
Palate ridges	5*	4*	5 - 5*	2
Upper tooth rows	42*	34*	33 - 38*	2
Lower tooth rows	45*	36*	35 - 38*	2
Total pectoral radials	118‡	116‡	112 - 117‡	2
Propterygial radials	56‡	57‡	53 - 55‡	2
Mesopterygial radials	15‡	15‡	12 - 17‡	2
Metapterygial radials	47‡	44‡	45 - 47‡	2
Total pelvic radials	26‡	18‡	19 - 20‡	2
Total vertebral segments	114‡	119‡	112 - 114‡	2
Monospondylous vertebrae	n.a	n.a	n.a - n.a	2
Prespine diplospondylous	n.a	n.a	n.a - n.a	2
Postspine diplospondylous	n.a	n.a	n.a - n.a	2

Table 5.4.3b. Measurements in % of disc width, for *H. oxyrhyncha* (Sauvage 1878). (D) MTUF 30002 (nontype, female, unspecified locality); (E) ZRC 42991 (female, Kapuas Basin); (F) ZRC 42992, ZRC 42984 (males, Kapuas Basin). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(D)	(E)	(F)			
			Range	N	Mean	S.D.
Disc width (mm)	120.0	127.0	124.0 - 173.0	2	148.50	34.65
Total length	405.8	n.a	412.7 - 412.7	1	412.72	
Disc length	117.5	116.5	117.3 - 120.2	2	118.75	1.99
Snout to pectoral insert	106.5	104.7	104.3 - 107.4	2	105.87	2.15
Disc thickness	n.a	11.1	10.9 - 12.3	2	11.61	0.98
Snout preorbital	38.2	38.6	38.6 - 39.8	2	39.20	0.91
Snout preorbital (horizontal)	37.9	37.9	37.3 - 38.2	2	37.74	0.61
Length pelvic-fin	25.1	24.4	25.2 - 26.0	2	25.60	0.57
Width across pelvic-fin base	14.0	16.0	13.2 - 14.1	2	13.66	0.66
Greatest width across pelvic-fins	49.2	42.9	n.a - n.a	2		
Cloaca origin to tail tip	304.9	n.a	314.2 - 314.2	1	314.23	
Tail width, axil of pelvics	5.9	7.6	8.3 - 8.8	2	8.58	0.32
Tail height, axil of pelvics	5.3	6.6	6.0 - 6.6	2	6.26	0.42
Pectoral insertion to sting origin	50.6	46.5	38.2 - 39.1	2	38.67	0.65
Cloaca origin to sting	54.8	49.9	43.7 - 43.8	2	43.72	0.06
Tail width, base of sting	2.5	3.1	3.6 - 3.9	2	3.76	0.24
Tail height, base of sting	3.7	3.2	3.5 - 4.1	2	3.81	0.37
Sting length	n.a	n.a	17.6 - 17.6	1	17.61	
Snout preoral	39.7	39.2	39.3 - 40.8	2	40.05	1.04
Mouth width	9.0	9.0	8.5 - 9.6	2	9.03	0.78
Distance between nostrils	10.8	10.9	10.6 - 10.9	2	10.79	0.21
Interorbital width	12.5	12.8	12.8 - 13.2	2	12.98	0.28
Intereye width	14.9	18.3	16.6 - 17.6	2	17.09	0.73
Snout to maximum width	56.6	63.4	62.0 - 62.2	2	62.08	0.14
Eye diameter	3.6	3.4	3.2 - 3.4	2	3.31	0.17
Orbit diameter	5.3	5.0	5.1 - 5.2	2	5.15	0.04
Spiracle length	7.0	6.5	6.5 - 7.2	2	6.88	0.46
Interspiracular width	16.9	18.3	17.2 - 18.9	2	18.04	1.17
Orbit and spiracle length	11.0	10.4	10.5 - 10.5	2	10.51	0.02

...continued

Table 5.4.3b. continued.

Nostril length	4.1	4.9	5.2 - 549.2	2	277.20	384.65
Snout prenasal	33.0	32.5	32.0 - 33.6	2	32.80	1.08
Nasal curtain width	10.4	12.3	12.5 - 12.9	2	12.70	0.34
Nasal curtain length	5.1	6.6	6.8 - 7.0	2	6.89	0.20
End of orbit to pectoral insertion	63.3	61.9	61.7 - 63.3	2	62.50	1.10
Snout to origin of cloaca	100.9	100.4	98.5 - 102.6	2	100.54	2.89
Width, 1st gill slit	3.0	2.7	3.1 - 3.2	2	3.15	0.09
Width, 3rd gill slit	3.3	3.0	2.8 - 3.5	2	3.15	0.51
Width, 5th gill slit	1.9	2.2	2.1 - 2.5	2	2.28	0.30
Head length	65.6	65.7	65.6 - 68.0	2	66.80	1.71
Distance between 1st gill slits	24.0	22.5	21.9 - 22.3	2	22.08	0.24
Distance between 5th gill slits	16.0	15.8	14.9 - 16.2	2	15.52	0.93
Cloaca length	4.8	5.8	4.5 - 4.5	2	4.50	0.04
Clasper, postcloaca length	x	x	12.2 - 12.3	2	12.25	
Clasper, length from pelvic axil	x	x	7.6 - 8.3	2	7.97	0.52

Table 5.4.4b. Counts and meristic values for *H. oxyrhyncha.*

	(D)	(E)	(F)	
			Range	N
Oral papillae (floor)	2	4	4 - 4	2
Palate ridges	n.a	n.a	n.a - n.a	2
Upper tooth rows	n.a	15	23 - 23	2
Lower tooth rows	n.a	24	26 - 26	2
Total pectoral radials	120	119-121	116 - 119	2
Propterygial radials	58	57-59	54 - 57	2
Mesopterygial radials	16	15	14 - 18	2
Metapterygial radials	46	47	46 - 46	2
Total pelvic radials	26-27	27-29	22 - 22	2
Total vertebral segments	111	104	103 - 108	2
Monospondylous vertebrae	40	38	34 - 35	2
Prespine diplospondylous	71	65	63 - 72	2
Postspine diplospondylous	n.a	1	1 - 6	2

Table 5.4.5. Measurements in % of disc width, for *H. signifer* Compagno & Roberts 1982. (A) range for holotype and five paratypes (Compagno & Roberts 1982); (B) neonatal male (nontype), Chao Phraya (Compagno & Roberts 1982); (C) ZRC 42547 (nontype, female, from Mekong Basin); (D) ZRC 42993 (nontype, immature male, Kapuas, Kalimantan); (E) ZRC 42647, ZRC 42648 (nontypes, immature males, Batang Hari, Sumatera). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(A)	(B)	(C)	(D)	(E)			
					Range	N	Mean	S.D.
Disc width (mm)	278-382	115.0	252.0	139.0	163.0 - 188.0	2	175.50	17.68
Total length	461-468	460.0	426.2	426.6	464.4 - 464.4	1	464.42	
Disc length	102-106	104.0	102.0	102.2	104.3 - 105.3	2	104.81	0.72
Snout to pectoral insert	76.9-85.3	86.1	86.7	88.7	89.2 - 89.3	2	89.26	0.12
Disc thickness	10.7-11.9	13.0	10.3	11.4	11.0 - 11.5	2	11.23	0.38
Snout preorbital	n.a	n.a	25.8	27.9	27.2 - 28.5	2	27.86	0.94
Snout preorbital (horizontal)	23.8-25.9	24.3	24.7	26.1	25.6 - 27.2	2	26.40	1.18
Length pelvic-fin	22.5-25.9	20.9	25.3	24.3	24.0 - 26.1	2	25.04	1.45
Width across pelvic-fin base	11.5-18.9	12.2	14.7	16.4	14.2 - 16.0	2	15.06	1.28
Greatest width across pelvic-fins	46.8-55.4	48.7	39.5	n.a	n.a - n.a	2		
Cloaca origin to tail tip	n.a	n.a	345.5	343.3	382.0 - 382.0	1	382.02	
Tail width, axil of pelvics	9.7-11.6	11.3	9.7	7.9	8.2 - 9.1	2	8.63	0.65
Tail height, axil of pelvics	6.6-8.2	n.a	6.6	6.4	6.1 - 6.7	2	6.42	0.47
Pectoral insertion to sting origin	n.a	n.a	34.0	40.6	35.1 - 35.1	1	35.13	
Cloaca origin to sting	n.a	n.a	38.2	45.8	41.7 - 41.7	1	41.66	
Tail width, base of sting	n.a	n.a	5.1	3.9	4.5 - 4.5	1	4.53	
Tail height, base of sting	n.a	n.a	4.5	3.8	4.3 - 4.3	1	4.26	
Sting 1 length	n.a	n.a	7.2	n.a	n.a - n.a	1		
Sting 2 length	x	x	7.6	x	x - x	1		
Snout preoral	24.2-26.3	27.8	25.7	28.2	26.4 - 28.6	2	27.51	1.59
Mouth width	7.3-8.7	6.1	6.1	6.4	5.9 - 6.1	2	5.99	0.10
Distance between nostrils	6.9-8.0	7.8	7.0	7.8	7.1 - 7.5	2	7.32	0.29
Interorbital width	9.3-10.2	12.2	11.2	11.6	11.0 - 11.2	2	11.09	0.15
Intereye width	n.a	n.a	15.2	15.5	16.5 - 16.6	2	16.58	0.09
Snout to maximum width	n.a	n.a	46.7	47.0	46.5 - 47.8	2	47.16	0.87
Eye diameter	2.1-2.9	3.3	2.7	3.4	3.4 - 3.7	2	3.55	0.25
Orbit diameter	3.7-4.8	5.2	4.1	5.3	5.0 - 5.4	2	5.22	0.32
Spiracle length	7.3-8.6	7.0	5.7	6.7	6.1 - 6.8	2	6.46	0.54
Interspiracular width	12.9-13.6	18.3	15.3	15.6	16.3 - 16.7	2	16.52	0.32
Orbit and spiracle length	n.a	n.a	8.2	9.4	8.4 - 9.1	2	8.79	0.49

...continued

Table 5.4.5. continued.

Nostril length	n.a	n.a	4.4	4.5	4.4 - 4.9	2	4.63	0.34
Snout prenasal	18.6-21.2	21.7	20.6	23.0	21.5 - 23.4	2	22.42	1.32
Nasal curtain width	4.3-6.1	5.2	5.0	5.4	5.2 - 5.7	2	5.44	0.34
Nasal curtain length	n.a	n.a	7.7	9.3	8.3 - 8.5	2	8.43	0.14
End of orbit to pectoral insertion	n.a	n.a	58.2	57.5	56.7 - 58.5	2	57.60	1.31
Snout to origin of cloaca	80.3-85.6	88.7	80.7	83.3	82.4 - 83.2	2	82.78	0.55
Width, 1st gill slit	3.1-3.8	1.7	2.9	2.9	2.6 - 2.7	2	2.64	0.10
Width, 3rd gill slit	n.a	n.a	3.0	3.3	2.9 - 2.9	2	2.89	0.06
Width, 5th gill slit	2.4-2.9	1.7	2.3	1.8	1.6 - 2.1	2	1.83	0.36
Head length	49.4-55.1	54.8	49.7	53.6	52.9 - 54.2	2	53.55	0.96
Distance between 1st gill slits	20.4-23.4	23.5	20.4	21.9	20.8 - 21.0	2	20.89	0.09
Distance between 5th gill slits	12.8-13.9	15.7	14.0	14.6	13.6 - 14.4	2	14.00	0.57
Cloaca length	n.a	n.a	4.7	4.4	3.6 - 4.7	2	4.15	0.78
Clasper, postcloaca length	n.a	n.a	x	11.2	11.8 - 13.4	2	12.60	1.19
Clasper, length from pelvic axil	n.a	n.a	x	7.3	7.0 - 9.3	2	8.13	1.59

Table 5.4.6. Counts and meristic values for *H. signifer*. [*high values attributed to different count methods (*see text*)].

	(A)	(B)	(C)	(D)	(E)	
					Range	N
Oral papillae (floor)	4(3) or 5(3)	4	4	2?	4 - 4	2
Palate ridges	n.a	n.a	n.a	n.a	n.a - n.a	2
Upper tooth rows	*38-45	*40	15	14	n.a - n.a	2
Lower tooth rows	*38-46	*37	n.a	18	n.a - n.a	2
Total pectoral radials	109-116	115	119	111	112 - 115	2
Propterygial radials	50-54	54	53-54	50	50 - 52	2
Mesopterygial radials	12-15	11	11-12	12	13 - 14	2
Metapterygial radials	45-48	50	54	49	48 - 49	2
Total pelvic radials	22-28	20?	25-26	24	21 - 22	2
Total vertebral segments	109-116	113	106	105	105 - 107	2
Monospondylous vertebrae	34-41	n.a	40	34	35 - 36	2
Prespine diplospondylous	n.a	n.a	56	70	58 - 70	2
Postspine diplospondylous	n.a	n.a	10	1	0 - 13	2

Table 5.4.7a. Measurements in % of disc width, for *H. walga* (Müller & Henle 1841). (A) MNHN 2438 (possible syntype, mature male); (B) MNHN 2431 (possible syntype, female); (C) MNHN 2337 (possible syntype, mature male); (D) BMNH 1867.11.28.158 (possible holotype of *T. heterurus*, female); (E) BMNH 1845.3.7.19, BMNH 1845.3.7.20 (possible syntypes of *T. nuda*, immature males). N is number of specimens from which means and standard deviations (S.D.) were taken. (*measurements by P. Last).

	(A)*	(B)*	(C)*	(D)*	(E)*			
					Range	N	Mean	S.D.
Disc width (mm)	158.9	170.4	172.2	162.5	94.9 - 104.7	2	99.83	6.91
Total length	197.6	231.2	296.2	213.6	254.0 - 254.9	2	254.47	0.61
Disc length	106.9	111.5	109.1	110.1	103.4 - 104.3	2	103.85	0.66
Snout to pectoral insert	98.6	101.0	n.a	98.9	94.7 - 94.9	2	94.78	0.13
Disc thickness	10.6	8.9	n.a	10.2	9.7 - 11.1	2	10.41	0.97
Snout preorbital	30.5	33.7	36.9	31.7	30.5 - 32.3	2	31.40	1.24
Snout preorbital (horizontal)	29.8	33.2	35.0	30.6	30.9 - 31.3	2	31.13	0.28
Length pelvic-fin	21.1	21.7	n.a	26.8	22.2 - 22.7	2	22.47	0.37
Width across pelvic-fin base	14.7	17.6	n.a	17.1	13.2 - 13.9	2	13.59	0.48
Greatest width across pelvic-fins	33.6	39.1	n.a	13.3	8.7 - 9.8	2	9.27	0.76
Cloaca origin to tail tip	106.4	137.1	n.a	122.1	164.1 - 165.9	2	165.03	1.26
Tail width, axil of pelvics	8.1	10.0	n.a	7.8	7.3 - 7.8	2	7.53	0.39
Tail height, axil of pelvics	5.4	7.0	n.a	6.6	5.1 - 5.4	2	5.25	0.25
Pectoral insertion to sting origin	26.3	31.9	n.a	28.7	30.9 - 31.4	2	31.13	0.38
Cloaca origin to sting	28.8	36.1	n.a	34.0	33.6 - 36.4	2	35.00	2.01
Tail width, base of sting	5.2	5.3	n.a	5.0	3.6 - 3.6	2	3.63	0.01
Tail height, base of sting	3.9	3.9	n.a	4.1	3.3 - 3.8	2	3.58	0.33
Sting 1 length	n.a	n.a	n.a	n.a	30.2 - 31.6	2	30.89	0.96
Sting 2 length	x	n.a	n.a	n.a	x - x	2		
Snout preoral	30.6	n.a	n.a	33.0	32.0 - 33.2	2	32.61	0.82
Mouth width	9.8	n.a	n.a	9.8	10.2 - 10.3	2	10.21	0.09
Distance between nostrils	11.8	n.a	n.a	11.7	11.5 - 11.5	2	11.52	0.02
Interorbital width	11.6	11.4	15.5	12.4	11.7 - 11.8	2	11.73	0.05
Intereye width	17.3	16.5	n.a	15.3	15.2 - 16.2	2	15.71	0.73
Snout to maximum width	48.2	52.0	n.a	50.3	45.0 - 50.6	2	47.79	3.99
Eye diameter	4.7	4.2	n.a	4.4	4.1 - 4.4	2	4.26	0.15
Orbit diameter	6.7	6.1	5.3	6.6	6.7 - 7.1	2	6.90	0.28
Spiracle length	6.2	7.2	n.a	5.5	6.3 - 6.6	2	6.45	0.17
Interspiracular width	15.5	16.6	19.3	16.7	16.5 - 17.4	2	16.95	0.70
Orbit and spiracle length	10.0	10.9	n.a	10.1	9.8 - 10.3	2	10.09	0.36

...continued

Table 5.4.7a. continued.

Nostril length	3.9	3.9	n.a	4.8	4.2 - 5.2	2	4.72	0.70
Snout prenasal	24.2	30.2	n.a	26.4	25.9 - 26.7	2	26.28	0.61
Nasal curtain width	11.4	n.a	n.a	11.6	11.5 - 12.3	2	11.88	0.60
Nasal curtain length	5.4	6.6	n.a	5.5	5.1 - 5.5	2	5.30	0.33
End of orbit to pectoral insertion	62.6	62.1	n.a	63.2	57.2 - 58.1	2	57.62	0.62
Snout to origin of cloaca	91.2	94.2	n.a	91.5	88.1 - 90.8	2	89.44	1.87
Width, 1st gill slit	2.3	2.5	n.a	3.1	2.1 - 2.2	2	2.14	0.09
Width, 3rd gill slit	2.5	2.4	n.a	3.5	2.7 - 3.1	2	2.91	0.28
Width, 5th gill slit	1.7	1.3	n.a	1.9	1.5 - 2.0	2	1.75	0.30
Head length	57.0	61.0	n.a	57.6	56.6 - 59.1	2	57.87	1.79
Distance between 1st gill slits	23.2	25.4	n.a	23.7	22.0 - 23.9	2	22.99	1.35
Distance between 5th gill slits	14.9	14.5	n.a	15.3	14.7 - 15.5	2	15.13	0.57
Cloaca length	5.4	5.1	n.a	5.7	4.6 - 5.5	2	5.06	0.59
Clasper, postcloaca length	18.0	x	n.a	x	9.2 - 11.4	2	10.29	1.53
Clasper, length from pelvic axil	7.0	x	n.a	x	2.6 - 3.0	2	2.77	0.25

Table 5.4.8a. Counts and meristic values for *H. walga*. (*counts by P. Last).

	(A)	(B)*	(C)*	(D)*	(E)	
					Range	N
Oral papillae (floor)	n.a	2	0?	2	n.a - n.a	2
Palate ridges	n.a	n.a	n.a	2	n.a - n.a	2
Upper tooth rows	n.a	*40	*44	2	n.a - n.a	2
Lower tooth rows	n.a	*50	n.a	2	n.a - n.a	2
Total pectoral radials	n.a	n.a	n.a	n.a	n.a - n.a	2
Propterygial radials	n.a	n.a	n.a	n.a	n.a - n.a	2
Mesopterygial radials	n.a	n.a	n.a	n.a	n.a - n.a	2
Metapterygial radials	n.a	n.a	n.a	n.a	n.a - n.a	2
Total pelvic radials	n.a	n.a	n.a	n.a	n.a - n.a	2
Total vertebral segments	n.a	n.a	n.a	n.a	n.a - n.a	2
Monospondylous vertebrae	n.a	n.a	n.a	n.a	n.a - n.a	2
Prespine diplospondylous	n.a	n.a	n.a	n.a	n.a - n.a	2
Postspine diplospondylous	n.a	n.a	n.a	n.a	n.a - n.a	2

Table 5.4.7b. Measurements in % of disc width, for *H. walga* (Müller & Henle 1841). (F) MTUF 29999 (nontype, female, India); (G) MTUF 29998 (nontype, mature male, Vietnam); (H) CSIRO H4426.11 (nontype, mature male; Muara Angke, Java); (I) CSIRO H4927.04 (nontype, female; Trang, Thailand). N is number of specimens from which means and standard deviations (S.D.) were taken.

	(F)	(G)	(H)	(I)
Disc width (mm)	184.0	176.0	200.0	210.0
Total length	n.a	n.a	n.a	176.2
Disc length	104.3	107.4	105.5	108.1
Snout to pectoral insert	95.1	98.0	96.2	98.7
Disc thickness	11.4	13.8	12.3	12.4
Snout preorbital	31.8	30.0	29.6	29.3
Snout preorbital (horizontal)	31.6	27.1	29.2	27.6
Length pelvic-fin	17.9	23.7	24.3	23.1
Width across pelvic-fin base	15.4	15.2	n.a	15.6
Greatest width across pelvic-fins	40.8	40.3	n.a	n.a
Cloaca origin to tail tip	n.a	n.a	n.a	85.2
Tail width, axil of pelvics	9.2	10.8	9.1	9.8
Tail height, axil of pelvics	6.1	6.0	5.6	5.5
Pectoral insertion to sting origin	32.7	n.a	n.a	21.3
Cloaca origin to sting	36.1	n.a	n.a	29.4
Tail width, base of sting	4.3	n.a	n.a	5.3
Tail height, base of sting	3.6	n.a	n.a	3.7
Sting 1 length	n.a	n.a	n.a	n.a
Sting 2 length	n.a	x	x	n.a
Snout preoral	32.8	29.7	30.5	30.9
Mouth width	n.a	n.a	10.3	10.0
Distance between nostrils	11.4	12.6	12.4	11.5
Interorbital width	11.4	12.5	10.5	11.7
Intereye width	15.6	16.9	16.6	16.3
Snout to maximum width	47.8	46.5	47.4	46.1
Eye diameter	3.6	4.1	3.3	3.8
Orbit diameter	5.8	6.5	5.5	5.8
Spiracle length	6.5	5.6	6.1	5.6
Interspiracular width	15.8	18.5	16.6	15.9
Orbit and spiracle length	10.1	10.7	10.3	10.3

...continued

Table 5.4.7b. continued.

Nostril length	4.1	3.6	4.4	5.2
Snout prenasal	26.4	23.0	24.0	23.9
Nasal curtain width	11.7	13.4	13.2	11.6
Nasal curtain length	6.2	7.6	7.6	7.1
End of orbit to pectoral insertion	58.8	62.9	62.1	64.2
Snout to origin of cloaca	90.9	91.4	88.7	91.0
Width, 1st gill slit	3.1	3.0	2.7	3.5
Width, 3rd gill slit	3.2	3.5	3.2	3.5
Width, 5th gill slit	2.1	2.0	2.0	2.2
Head length	57.5	58.2	57.1	56.2
Distance between 1st gill slits	22.4	25.2	23.8	23.4
Distance between 5th gill slits	13.0	16.9	15.2	14.9
Cloaca length	4.8	5.9	5.0	5.2
Clasper, postcloaca length	x	19.2	18.7	x
Clasper, length from pelvic axil	x	13.6	13.3	x

Table 5.4.8b. Counts and meristic values for *H. walga*.

	(F)	(G)	(H)	(I)
Oral papillae (floor)	n.a	n.a	n.a	n.a
Palate ridges	n.a	n.a	n.a	n.a
Upper tooth rows	n.a	n.a	n.a	n.a
Lower tooth rows	n.a	n.a	n.a	n.a
Total pectoral radials	101-102	101	n.a	98-103
Propterygial radials	46	45-46	n.a	48
Mesopterygial radials	12	11-12	n.a	10-12
Metapterygial radials	43-44	44	n.a	43-44
Total pelvic radials	22	17	n.a	18-22
Total vertebral segments	96	n.a	n.a	91
Monospondylous vertebrae	35	n.a	n.a	38
Prespine diplospondylous	52	n.a	n.a	41
Postspine diplospondylous	9	n.a	n.a	12

Table 5.4.7c. Measurements in % of disc width, for *H. walga* (Müller & Henle 1841). (J) CSIRO H4924.02, CSIRO H4924.04, CSIRO H4924.05, CSIRO H4924.10, CSIRO H4924.11, CSIRO H4924.14 (nontype, males); (K) CSIRO H4924.01, CSIRO H4924.03, CSIRO H4924.06, CSIRO H4924.07, CSIRO H4924.08, CSIRO H4924.09, CSIRO H4924.12, CSIRO H4924.13 (nontype, females). Locality: Prachuap Khiri Khan, Thailand. N is number of specimens from which means and standard deviations (S.D.) were taken.

	(J)				(K)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	66.0 - 187.0	6	158.42	45.62	161.0 - 199.0	8	179.88	13.72
Total length	215.3 - 262.1	5	229.95	18.95	156.3 - 205.3	8	182.74	14.68
Disc length	103.1 - 107.6	6	104.92	1.95	105.3 - 110.6	8	108.26	1.85
Snout to pectoral insert	93.5 - 98.2	6	95.41	1.84	95.7 - 102.1	8	98.93	1.92
Disc thickness	11.8 - 13.5	6	12.92	0.63	10.9 - 13.1	8	12.38	0.69
Snout preorbital	24.1 - 30.1	6	28.23	2.21	28.8 - 31.3	8	29.75	0.81
Snout preorbital (horizontal)	21.7 - 29.5	6	27.10	2.76	25.6 - 29.0	8	27.78	1.07
Length pelvic-fin	18.6 - 24.5	6	22.24	1.98	18.6 - 24.0	8	22.42	1.81
Width across pelvic-fin base	13.8 - 15.5	6	14.59	0.64	15.4 - 17.8	8	16.88	0.90
Greatest width across pelvic-fins	40.6 - 42.5	3	41.80	1.00	37.0 - 42.1	3	38.97	2.72
Cloaca origin to tail tip	122.4 - 171.4	5	139.27	19.44	64.3 - 116.4	8	90.49	15.90
Tail width, axil of pelvics	8.2 - 9.1	6	8.72	0.31	9.2 - 11.2	8	10.01	0.68
Tail height, axil of pelvics	5.3 - 6.7	6	5.80	0.51	5.4 - 6.6	8	5.93	0.45
Pectoral insertion to sting origin	20.2 - 36.6	6	25.91	5.67	20.7 - 31.0	8	24.19	3.05
Cloaca origin to sting	22.2 - 40.1	6	29.91	5.76	28.8 - 35.4	8	30.61	2.00
Tail width, base of sting	4.1 - 5.6	6	5.10	0.59	3.5 - 5.9	8	5.32	0.76
Tail height, base of sting	3.3 - 3.9	6	3.69	0.27	2.7 - 4.2	8	3.67	0.48
Sting 1 length	11.5 - 11.5	1	11.52		n.a - n.a	7		
Sting 2 length	n.a - n.a	5			n.a - n.a	7		
Snout preoral	27.4 - 31.6	6	29.47	1.61	29.8 - 32.8	8	30.99	0.85
Mouth width	9.0 - 10.0	6	9.58	0.39	8.3 - 10.2	8	9.00	0.56
Distance between nostrils	12.2 - 13.1	6	12.67	0.31	10.8 - 11.4	8	11.04	0.23
Interorbital width	10.1 - 12.3	6	10.90	0.90	10.0 - 11.6	8	10.94	0.63
Intereye width	16.2 - 22.0	6	17.65	2.16	15.7 - 16.8	8	16.35	0.37
Snout to maximum width	39.7 - 49.1	6	44.90	3.11	46.5 - 50.5	8	48.44	1.51
Eye diameter	4.1 - 5.0	6	4.39	0.34	3.8 - 4.6	8	4.28	0.26
Orbit diameter	6.2 - 8.3	6	7.19	0.70	6.3 - 7.9	8	7.09	0.61
Spiracle length	4.9 - 10.0	6	6.23	1.90	5.5 - 6.2	8	5.94	0.26
Interspiracular width	16.7 - 19.7	6	17.48	1.11	15.5 - 16.4	8	16.04	0.38
Orbit and spiracle length	10.1 - 13.0	6	11.01	1.04	5.0 - 10.9	8	9.73	1.94

...continued

Table 5.4.7c. continued.

Nostril length	4.0 - 4.9	6	4.51	0.34	4.4 - 5.1	8	4.68	0.25
Snout prenasal	21.4 - 25.0	6	23.32	1.25	23.4 - 26.6	8	24.89	0.90
Nasal curtain width	10.8 - 13.8	6	12.82	1.03	11.0 - 12.6	8	11.67	0.48
Nasal curtain length	6.7 - 8.2	6	7.37	0.64	6.3 - 7.1	8	6.81	0.28
End of orbit to pectoral insertion	59.5 - 62.1	6	60.65	0.96	60.0 - 65.0	8	62.77	1.71
Snout to origin of cloaca	85.5 - 93.2	6	89.82	3.01	88.9 - 95.6	8	92.25	2.28
Width, 1st gill slit	2.7 - 4.1	6	3.37	0.50	2.6 - 3.2	8	2.93	0.18
Width, 3rd gill slit	3.1 - 4.3	6	3.65	0.44	3.1 - 3.7	8	3.33	0.23
Width, 5th gill slit	1.9 - 2.6	6	2.17	0.25	1.9 - 2.5	8	2.09	0.20
Head length	55.1 - 58.8	6	56.62	1.61	55.1 - 57.5	8	56.30	0.80
Distance between 1st gill slits	23.0 - 24.4	6	23.97	0.50	22.3 - 24.4	8	23.33	0.66
Distance between 5th gill slits	14.6 - 16.5	6	15.83	0.71	14.6 - 16.6	8	15.44	0.58
Cloaca length	4.5 - 5.2	6	4.81	0.30	4.9 - 7.2	8	5.94	0.86
Clasper, postcloaca length	11.1 - 22.8	6	19.96	4.44	x - x	8		
Clasper, length from pelvic axil	8.2 - 17.1	6	14.81	3.35	x - x	8		

Table 5.4.8c. Counts and meristic values for *H. walga*.

	(J)		(K)	
	Range	N	Range	N
Oral papillae (floor)	n.a - n.a	6	2 - 2	1
Palate ridges	n.a - n.a	6	n.a - n.a	1
Upper tooth rows	n.a - n.a	6	n.a - n.a	1
Lower tooth rows	n.a - n.a	6	n.a - n.a	1
Total pectoral radials	102 - 104	2	103 - 107	3
Propterygial radials	45 - 50	2	46 - 49	3
Mesopterygial radials	11 - 13	2	11 - 15	3
Metapterygial radials	42 - 44	2	43 - 46	3
Total pelvic radials	17 - 19	2	24 - 26	3
Total vertebral segments	85 - 87	2	87 - 92	3
Monospondylous vertebrae	39 - 40	2	38 - 43	3
Prespine diplospondylous	38 - 38	2	39 - 42	3
Postspine diplospondylous	8 - 9	2	5 - 11	2

Table 5.4.7d. Measurements in % of disc width, for *H. walga* (Müller & Henle 1841). (J) CSIRO H5471.04, CSIRO H5471.05, CSIRO H5471.06, CSIRO H5471.07, CSIRO H5473.02, CSIRO H5474.01, CSIRO H5474.02, CSIRO H5474.19, CSIRO H5474.20, CSIRO H5584.09 (nontype, males); (K) CSIRO H5473.01, CSIRO H5474.14, CSIRO H5474.15, CSIRO H5474.16, CSIRO H5474.17, CSIRO H5474.18, CSIRO H5584.07, CSIRO H5584.08, UMS MMKK11 (nontype, females). Locality: Kota Kinabalu, Sabah, Malaysia. N is number of specimens from which means and standard deviations (S.D.) were taken.

	(L)				(M)			
	Range	N	Mean	S.D.	Range	N	Mean	S.D.
Disc width (mm)	101.0 - 200.0	10	166.10	36.99	136.0 - 210.0	9	182.06	28.44
Total length	197.9 - 255.1	9	232.84	16.05	184.9 - 215.6	7	200.10	13.64
Disc length	103.7 - 108.0	10	105.21	1.57	103.3 - 109.8	9	106.57	2.39
Snout to pectoral insert	92.7 - 98.3	10	94.61	1.77	92.9 - 101.8	9	96.73	3.27
Disc thickness	11.2 - 13.4	10	12.45	0.84	10.6 - 13.2	9	12.06	0.89
Snout preorbital	29.5 - 32.0	10	30.83	0.74	28.3 - 32.9	9	30.67	1.38
Snout preorbital (horizontal)	28.2 - 30.6	10	29.49	0.84	27.0 - 31.4	9	29.60	1.36
Length pelvic-fin	19.0 - 24.1	10	22.15	1.53	20.0 - 23.3	9	21.61	1.20
Width across pelvic-fin base	12.9 - 15.2	10	13.83	0.62	12.8 - 18.7	8	16.15	1.94
Greatest width across pelvic-fins	42.2 - 42.2	1	42.22		32.1 - 32.1	1	32.15	
Cloaca origin to tail tip	108.5 - 168.3	9	144.38	16.70	93.1 - 127.8	7	110.86	14.65
Tail width, axil of pelvics	8.1 - 10.4	10	9.46	0.75	9.2 - 11.2	9	10.50	0.63
Tail height, axil of pelvics	5.0 - 6.5	10	5.74	0.44	4.9 - 6.5	9	5.74	0.61
Pectoral insertion to sting origin	24.0 - 32.1	9	27.68	2.66	23.7 - 30.9	7	27.17	2.53
Cloaca origin to sting	28.4 - 37.1	9	32.02	2.49	29.7 - 35.6	7	32.90	2.26
Tail width, base of sting	3.5 - 6.4	9	4.96	0.94	4.1 - 5.4	7	4.78	0.57
Tail height, base of sting	2.7 - 4.0	9	3.37	0.40	2.7 - 3.6	7	3.30	0.37
Sting 1 length	n.a - n.a	9			? - ?	9		
Sting 2 length	n.a - n.a	9			? - ?	9		
Snout preoral	29.5 - 33.1	10	31.31	1.07	29.1 - 33.0	9	31.56	1.24
Mouth width	8.8 - 9.9	10	9.40	0.39	7.9 - 8.8	9	8.47	0.27
Distance between nostrils	11.3 - 13.2	10	12.03	0.52	10.4 - 11.1	9	10.77	0.23
Interorbital width	10.5 - 13.0	10	12.29	0.72	10.9 - 11.6	9	11.30	0.30
Intereye width	15.9 - 18.6	10	17.44	0.88	16.1 - 17.5	9	16.56	0.42
Snout to maximum width	45.4 - 51.9	10	48.68	1.86	39.8 - 51.4	9	45.84	3.32
Eye diameter	3.9 - 4.7	10	4.22	0.29	3.7 - 4.5	9	4.10	0.22
Orbit diameter	5.9 - 7.0	10	6.30	0.32	5.8 - 6.6	9	6.12	0.22
Spiracle length	5.5 - 6.9	10	6.24	0.41	5.2 - 6.6	9	5.61	0.44
Interspiracular width	16.7 - 18.0	10	17.13	0.39	15.4 - 16.8	9	16.13	0.41
Orbit and spiracle length	10.0 - 11.3	10	10.47	0.49	9.4 - 10.8	9	9.90	0.44

...continued

Table 5.4.7d. continued.

Nostril length	3.5 - 5.2	10	4.38	0.44	4.2 - 5.0	9	4.57	0.30
Snout prenasal	23.5 - 26.7	10	25.20	1.01	24.2 - 27.6	9	25.53	1.07
Nasal curtain width	11.2 - 14.1	10	12.67	0.86	10.9 - 11.7	9	11.24	0.27
Nasal curtain length	6.4 - 7.1	10	6.76	0.23	5.3 - 6.9	9	6.23	0.47
End of orbit to pectoral insertion	55.7 - 62.0	10	59.02	2.05	56.9 - 65.7	9	61.07	3.38
Snout to origin of cloaca	86.8 - 92.3	10	88.73	1.77	85.0 - 92.9	9	89.64	2.68
Width, 1st gill slit	2.7 - 3.6	10	3.01	0.28	2.6 - 3.4	9	3.02	0.26
Width, 3rd gill slit	2.9 - 3.7	10	3.35	0.28	2.9 - 3.6	9	3.28	0.26
Width, 5th gill slit	1.7 - 2.3	10	1.92	0.19	1.6 - 2.7	9	2.17	0.32
Head length	56.4 - 59.3	10	57.68	1.03	52.9 - 57.6	9	56.03	1.54
Distance between 1st gill slits	21.2 - 25.1	10	23.03	1.02	21.0 - 22.4	9	21.78	0.44
Distance between 5th gill slits	14.7 - 16.5	10	15.56	0.56	14.1 - 15.3	9	14.76	0.42
Cloaca length	4.0 - 5.6	10	4.90	0.51	4.5 - 7.3	9	5.94	1.03
Clasper, postcloaca length	12.0 - 22.6	10	19.35	3.73	x - x	9		
Clasper, length from pelvic axil	7.5 - 20.3	10	14.37	4.03	x - x	9		

Table 5.4.8d. Counts and meristic values for *H. walga*.

	(L)		(M)	
	Range	N	Range	N
Oral papillae (floor)	2 - 3	3	3 - 3	3
Palate ridges	n.a - n.a	3	n.a - n.a	3
Upper tooth rows	n.a - n.a	3	n.a - n.a	3
Lower tooth rows	n.a - n.a	3	n.a - n.a	3
Total pectoral radials	100 - 105	8	103 - 106	5
Propterygial radials	46 - 50	8	49 - 50	5
Mesopterygial radials	9 - 15	8	10 - 12	5
Metapterygial radials	40 - 45	8	42 - 47	5
Total pelvic radials	15 - 20	8	21 - 24	5
Total vertebral segments	84 - 94	8	86 - 93	5
Monospondylous vertebrae	35 - 40	8	35 - 37	5
Prespine diplospondylous	41 - 56	8	42 - 57	5
Postspine diplospondylous	0 - 8	8	0 - 8	5

Table 5.4.9. Measurements in % of disc width, for *H.* sp. G. (*tail tip damaged).

	MTUF 30001
Disc width (mm)	231.0
Total length	*292.6
Disc length	113.9
Snout to pectoral insert	99.4
Disc thickness	16.0
Snout preorbital	31.2
Snout preorbital (horizontal)	30.5
Length pelvic fin	27.2
Width across pelvic-fin base	15.7
Greatest width across pelvic-fins	49.9
Cloaca origin to tail tip	*203.1
Tail width, axil of pelvics	10.7
Tail height, axil of pelvics	7.4
Pectoral insertion to sting origin	27.9
Cloaca origin to sting	39.0
Tail width, base of sting	5.6
Tail height, base of sting	4.6
Sting 1 length	18.6
Sting 2 length	26.8
Snout preoral	31.2
Mouth width	6.6
Distance between nostrils	8.4
Interorbital width	12.7
Intereye width	16.0
Snout to maximum width	54.0
Eye diameter	3.5
Orbit diameter	4.8
Spiracle length	6.8
Interspiracular width	17.3
Orbit and spiracle length	9.9

...continued

Table 5.4.9. continued.

Nostril length	5.1
Snout prenasal	24.6
Nasal curtain width	10.0
Nasal curtain length	6.4
End of orbit to pectoral insertion	64.2
Snout to origin of cloaca	89.5
Width, 1st gill slit	3.7
Width, 3rd gill slit	3.8
Width, 5th gill slit	2.3
Head length	58.7
Distance between 1st gill slits	24.4
Distance between 5th gill slits	18.3
Cloaca length	5.0
Clasper, postcloaca length	22.2
Clasper, length from pelvic axil	13.0

Table 5.4.10. Counts and meristic values for *H.* sp. G.

	MTUF 30001
Oral papillae (floor)	2
Palate ridges	3
Upper tooth rows	24
Lower tooth rows	22
Total pectoral radials	110-111
Propterygial radials	49
Mesopterygial radials	12-13
Metapterygial radials	48-50
Total pelvic radials	22
Total vertebral segments	n.a
Monospondylous vertebrae	n.a
Prespine diplospondylous	n.a
Postspine diplospondylous	n.a

APPENDICES

APPENDIX 2.1.1. Flowchart of in-situ market sampling strategy

Checklist all stingray taxa observed. Measure disc width (DW) for single individuals of a species; if more than one individual, estimate the average measurement. All measurements expressed in millimeters (mm). Maturity stages of the male specimens are estimated using the alphanumeric notation system (Smale & Compagno *in* Compagno 1988). (*Auxiliary Table 2.1.1a*)

⇩

For specimens up to 500 mm DW, purchase them (at least 5 specimens of the same sex of each comparable semaphoront and at least an additional specimen for dissecting purposes should be saved). These are treated later (in laboratory).

For individuals more than 500 mm DW, these are too bulky to be transported and may be too expensive to purchase whole. Treatment of such specimen is as follows.

⇩

Photograph the fish for the following parts: dorsal surface (whole fish, indicating disc shape; close-up of the skin, indicating squamation), and ventral surface (oronasal area; close-up of the pelvic fins including the claspers, indicating shape).

⇩

Obtain a sample of muscle tissue (from fresh specimens). A strategy for collecting tissue samples is given in Auxiliary Table 2.1.1b.

⇩

Obtain basic morphometrics before fish is chopped up. These include DW, disc length (DL), and total length (TL). Weight of the fish is also obtained if possible.

⇩

Save the body parts normally discarded by fish-sellers i.e. head and trunk (pectoral girdle, pelvic girdle, and pelvic fins including the claspers). Skin sample containing dermal denticles from across the disc is saved if possible.

APPENDIX 2.1.1 (continued)

Auxiliary Table 2.1.1a.

i) Field Journal

General Location ______________________ Date ________ ______________________ Time ________ Lat __________ Long __________ Other observations ______________________ Total # species __________ Total # individuals ________				
species	Log 3	DW (mm)	Sex/ Maturity	Notes

ii) Logarithmic abundance categories used to estimate the abundance of numerically dominant fish species (Russ 1985)

Log 3 Abundance Category	Number of Fishes
1	1
2	2-3
3	4-9
4	10-27
5	28-81

iii) Alphanumeric notation system for estimating elasmobranch maturity stages (Smale & Compagno *in* Compagno 1988).

M	male
F	female
1	embryo or foetus
2	immature
3	adolescent
4	adult

Note: Numbers are sometimes "hedged" to indicate transitional stage, e.g. M2-3 is a male just starting adolescence, and M3-4 is a male in the latest adolescence or preadulthood.

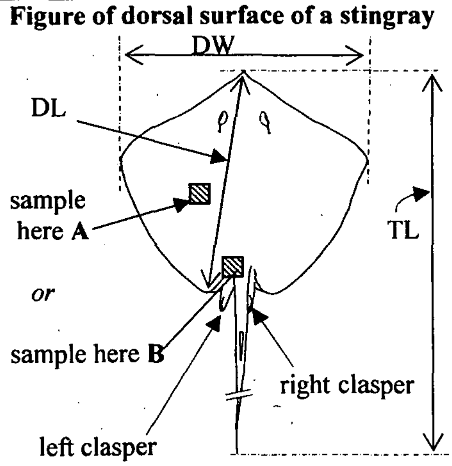
Using this system, the maturity stages of females cannot be ascertained without having to cut open the abdomen to examine the condition of the uterus. However, it was not possible to do this for most of the specimens examined. The maturity stage of a female specimen may be arbitrarily determined when males of similar size range occur together, assuming that fishes landed together are of comparable semaphoront. Studies have shown that the males mature earlier than the females of the same species, i.e. males are mature at a smaller size and at an earlier age than females (e.g. Devadoss 1978; Cowley 1997).

APPENDIX 2.1.1 (continued)

Auxiliary Table 2.1.1b. Protocol for collecting stingray tissue samples and whole specimens.

A copy of this protocol was given out to individual personnels in seeking their assistance to collect tissues samples and specimens.

Figure of dorsal surface of a stingray



What you will need:
Clean scalpel blades or pen knife, clean 1.5 ml vials half-filled with 90% ethanol, smear-proof marker points, measuring ruler, log book and ball-point pen, paper towels, camera.

Where to sample:

A: on pectoral fin
B: on lateral surface of tail just forward of the base of the tail

-Indicate on the label, which part the tissue was taken from.

A. Tissue samples (see figure)

1. Must be obtained from fresh or freshly killed fish only, because protein deteriorates rapidly after death and will affect quality of DNA.

2. It is also very important to collect clean uncontaminated tissue samples. This is done by cutting deeply into the flesh, and cut out about 0.5 cm^2 of tissue and placing it directly into a sample vial containing 90% ethanol. Label the vial and indicate which part the tissue was taken from. Store away from heat, preferably in shade. Use a new blade for each specimen or if same blade/knife is used, sterilize it by wiping the 'contaminated' edges with an alcohol soaked paper towel before re-use.

3. If the specimen is too large to be saved, take the following basic measurements: disc width (DW), disc length (DL), and total length (TL), and indicate the unit of measurement used.

4. Include any other description or observations you may have on the specimen (e.g. colour of dorsal and ventral surfaces, patterning, squamation, number caught, etc.)

B. Stingray specimen

1. Small sized specimens (≤500 mm DW) are preferred. Fix them in 10% formalin (it helps to inject some formalin into the flesh through the thick skin; or make small slits through the thick skin when fixing the specimen). After at least a week in formalin, rinse thoroughly with (tap) water and transfer to 70% ethanol for permanent storage.

2. For the larger sized specimens (>500 mm DW), save the undamaged head part, and trunk (which includes the pectoral girdle, pelvic girdle, and left clasper). To give an idea, cut out the mid-portion from about the third quarter (from the snout tip) of the disc. All these are also fixed in 10% formalin for up to 3 days, then transfer into ethanol for longer term storage.

3. Include any other observations you may have on the specimen (e.g. colour of dorsal and ventral surfaces, patterning, squamation, etc.)

4. Include the locality of the specimen, and information about the area (e.g. bottom substrate, water depth, fishing gear etc.).

APPENDIX 2.1.2. Materials examined. Listing follows species name (in alphabetical order), specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see also Chapter 4, Appendix 4.1.1), [?]tentative identification pending further study (listed last under each species heading). Type specimens are indicated. [East Indies — name formerly applied to southeastern Asia, embracing the Indian subcontinent].

INGROUP

Indo-Pacific *Himantura*

1. H. chaophraya.—
CSIRO H2503.01[a] (Pentecost River, WA, Australia); CSIRO H2524.01 (Gilbert River, QLD, Australia); CSIRO H5283.01[a], SMKK KTG2-23397, SMKK KTG3-20497, SMKK KTG7-21096, UMS MMKG1 (Kinabatangan River, Sabah, Malaysia); MTUF 30233 (Rajmehar, India); MTUF 30203[e] (Bhagalpur, India); MTUF 30204[e], MTUF 30205, MTUF 30206 (Chao Phraya River, Thailand); RMNH 3365[c] (unspecified locality); RMNH-T 7452[c] (holotype of *Trygon polylepis*) (Java, Indonesia); SMKK BFT1-697[e] (Padas River, Sabah, Malaysia); SMKK SKN10-15697[e] (Sandakan, Sabah, Malaysia).

2. H. fai.—
CAS 213286(3of3), CAS 213290 (Thailand); CSIRO H687.2, CSIRO H1489.2 CSIRO H1910.1, CSIRO H5671.01 (NW Shelf, WA, Australia); CSIRO H2753.01, CSIRO H2754.01, CSIRO H2756.01 (Heron Island, QLD, Australia); CSIRO H3355.01, CSIRO H3378.01, CSIRO H5207.01[a,e] (G of Carpentaria, QLD, Australia); CSIRO H4426.33[b] (Java, Indonesia); CSIRO H5480.01[b,e] (Sandakan, Sabah, Malaysia); MTUF 26717 (Micronesia); USNM 51712[c,d] (holotype) (Apia, Samoa).

3a. H. gerrardi: var 'small denticle'—
BMNH 1843.5.19.1[c] (syntype of *Trygon gerrardi*), BMNH 1846.11.18.49[c] (syntype of *T. gerrardi*) (India); BMNH 1867.11.28.160[c] (possible syntype of *Trygon macrurus*) ('East Indies Archipelago'); CSIRO H4919.01, CSIRO H4919.03, CSIRO H5479.04, CSIRO H5479.09, CSIRO H5479.10, SMKK SKN22-4496, UMS MMSK35[e], UMS MMSK36[e], UMS MMSK37[e], UMS MMSK38, UMS MMSK(c7)[c,?], UMS MMSK(c8)[c,?] (Sandakan, Sabah, Malaysia); CSIRO H4122.01, CSIRO H4122.02, CSIRO H4123.01 (off Beruwala, Sri Lanka); CSIRO H4426.20, CSIRO H4426.21, CSIRO H4426.22, CSIRO H4426.23, CSIRO H4426.24 (Java, Indonesia); CSIRO H4922.01, CSIRO H4922.02, CSIRO H4922.03, CSIRO H5284.01, CSIRO H5284.02, CSIRO H5284.03[a], CSIRO H5284.04[b], CSIRO H5474.03, CSIRO H5474.04, CSIRO H5474.05, CSIRO H5474.06, CSIRO H5474.07, CSIRO H5474.08, CSIRO H5474.09, CSIRO H5474.10, CSIRO H5474.11, CSIRO H5474.12, CSIRO H5474.13, CSIRO H5476.01[e], CSIRO H5476.02[e], CSIRO H5476.04, CSIRO H5476.05, CSIRO H5476.06, CSIRO H5476.07, CSIRO H5584.01, CSIRO H5584.02, CSIRO H5584.03, CSIRO H5584.04, CSIRO H5584.05, CSIRO H5584.06, CSIRO H5584.10, CSIRO H5612.01, UMS MMKK24[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H4926.09, CSIRO H4926.10 (Nakhon Si Thammarat, Thailand); CSIRO H4927.05, H4927.07 (Trang, Thailand); MNHN A-7920[c] (India); MTUF 30004 (Thailand); NMV A949 (possible syntype of *T. macrurus*)(Indonesia); RMNH 2460[c], RMNH 2468[c], RMNH 2469[c], RMNH 7438(1)[c], RMNH 7438(2)[c], RMNH 7442(1)[c] (possible syntype of *T. macrurus*) ('East Indies'); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia); RMNH 7442(2)[?] (possible syntype of *T. macrurus*), RMNH 7442(3)[?] (possible syntype of *T. macrurus*) ('East Indies'); UMS MMSK(c7)[c,?], UMS MMSK(c8)[c,?] (Sandakan, Sabah, Malaysia).

3b. H. gerrardi: var 'large denticle'—
CSIRO H4919.02, CSIRO H5479.05, CSIRO H5479.06, CSIRO H5479.07, CSIRO H5479.11 (Sandakan, Sabah, Malaysia); CSIRO H4918.02[a], CSIRO H5482.04, CSIRO H5482.05, UMS MMT1[e], UMS MMT5, UMS MMT10 (Tawau, Sabah, Malaysia); CSIRO H5484.02, CSIRO H5484.03, CSIRO H5484.04, CSIRO H5484.05, CSIRO H5484.06, CSIRO H5484.07, CSIRO H5617.02, CSIRO H5617.03, CSIRO H5617.04, CSIRO H5617.05, CSIRO H5618.01[?] (Semporna, Sabah, Malaysia).

4. H. granulata.—
AMS I9763 (holotype) (New Guinea); BMNH 1879.5.22.105[c] (holotype of *Trygon ponapensis*) (Kubary, Ponapé); CAS 52032 (Palau); CSIRO CA1255 (N of Anson Bay, WA, Australia); CSIRO H962.1, NTM S.10718.062 (NT, Australia); CSIRO H2751.01 (Groote Eylandt, NT, Australia); CSIRO H3864.01 (E of Cape York Peninsula, QLD, Australia); CSIRO H4417.01 (NE of Shelburne Bay, QLD, Australia); CSIRO H4426.32[a] (Java, Indonesia); MTUF 26700, MTUF 26703, MTUF 26719, MTUF 26903[e], MTUF 26906 (Micronesia); QM I5879, QM I20184 (QLD, Australia); SMF 4747[d] (Maldives); SUML JPAG207 (Philippines).

5. H. imbricata.—
BPBM 33199(1of2), BPBM 33199(2of2) (Kuwait); CAS 141045 (mouth of Ganges River, India); LACM 38129-83(1of3), LACM 38129-83(2of3), LACM 38129-83(3of3), LACM 38130-60(1of10), LACM 38130-60(2of10), LACM 38130-60(3of10), LACM 38130-60(4of10), LACM 38314-24, LACM 38134-37(1of2) (Pakistan); NTM S.13160.009 (Chilaw, Sri Lanka); RMNH 7446[c] (holotype of *Trygon dadong*) (Bintang, Indonesia); ZMB 7585[c] (holotype) (Coromandel, India).

6. H. jenkinsii.—
CAS 213283, CAS 213284, CAS 213286(1of3), CAS 213286(2of3) (Thailand); CSIRO CA3947, CSIRO H4004.05[b] (NW shelf, WA, Australia); CSIRO H2906.01[a] (Arafura Sea, NT, Australia); CSIRO H3375.01, CSIRO H3622.01[a], CSIRO H3649.01 (G of Carpentaria, Australia); CSIRO H4123.02, CSIRO H5585.01[b] (off Beruwela, Sri Lanka); CSIRO H4918.01 (Tawau, Sabah, Malaysia); CSIRO H5475.01[a,e] (Kota Kinabalu, Sabah, Malaysia); SUML BRU116, SUML JPAG213[e] (Philippines).

7. H. oxyrhyncha.—
MNHN 9639[c] (holotype) (Saigon, Vietnam); MNHN 1922-77[c], MNHN 1922-78[c], MNHN 1922-79[c] (syntypes of *H. krempfi*) (Phnom Penh, Vietnam); MTUF 30002 (Thailand); ZRC 42984[a], ZRC 42991, ZRC 42992[e] (Kapuas Basin, Kalimantan, Indonesia).

8. H. pastinacoides.—
BMNH 1867.11.28.155[c] (holotype of *Trygon pareh*), BMNH 1867.11.28.161[c] (holotype of *Trygon pastinacoides*) ('Far East Indies'); CAS 213285 (Thailand); CSIRO H4424.01, CSIRO H4424.02, CSIRO H4424.03, CSIRO H5613.01[b,c] (Kuching, Sarawak, Malaysia); CSIRO H4426.01 (Java, Indonesia); CSIRO H5471.01[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H4921.04 [b], CSIRO H5479.02[b,c], CSIRO H5479.03, CSIRO H5479.12, CSIRO H5479.13, CSIRO H5479.14, CSIRO H5479.15, CSIRO H5480.02, CSIRO H5614.01[b,c], CSIRO H5615.01, CSIRO H5615.02, UMS MMSK7, UMS MMSK39, UMS MMSK40, UMS MMSK(26/3B) (Sandakan, Sabah, Malaysia); NMV A914 (Indonesia); RMNH 2461[c], RMNH 2463[c], RMNH 2464[c], RMNH 2470[c], RMNH 7437[c], RMNH 8007[c] (unspecified locality).

9. H. signifier.—
USNM 229492[c] (paratype) (Sintang, Kapuas River, Indonesia); ZRC 42547[a,e] (Mekong Basin, Thailand); ZRC 42647[e], ZRC 42648[e] (Batang Hari, Sumatra, Thailand); ZRC 42993 (Kapuas Basin, Kalimantan, Indonesia).

10. H. toshi.—
AMS IA39 (holotype) (Clarence River estuary, NSW, Australia); CSIRO CA2405, CSIRO CA2406, CSIRO CA4271, CSIRO H312.1, CSIRO H635.1, CSIRO H635.03, CSIRO H635.04, CSIRO H959.1, CSIRO H959.2, CSIRO H959.4, CSIRO H963.1, CSIRO H963.2, CSIRO H963.3, CSIRO H964.1, CSIRO H964.2, CSIRO H3380.01, CSIRO H3380.02, CSIRO H3381.01, CSIRO H3381.02, CSIRO H3381.03, CSIRO H3383.01, CSIRO H3387.01[e], CSIRO H3387.02, CSIRO H3387.03, CSIRO H5204.01, CSIRO H5205.01, CSIRO H5206.01, CSIRO H5586.01, CSIRO H5586.02[b], CSIRO H5586.03[b], CSIRO H5586.04[b], CSIRO H5589.01[b], CSIRO T698, CSIRO T699, CSIRO T700, NTM S.12416.001 (NT, Australia); CSIRO CA1245, CSIRO CA3994, CSIRO H1034.1, CSIRO H1034.2, CSIRO H1464.4, CSIRO H5587.01[b], CSIRO H1041.02, CSIRO H4077.01, CSIRO H4077.02, CSIRO H4077.03, CSIRO H4077.04, CSIRO H4083.01, WAM P29180.001 (NW Shelf, WA, Australia); CSIRO H1220.01[a], CSIRO H1220.2, CSIRO H1222.1[a], CSIRO H1222.2, CSIRO H3322.02, CSIRO H3329.01, CSIRO H3352.01[e], CSIRO H3369.01,

CSIRO H3373.01, CSIRO H3373.02, CSIRO H3373.03, CSIRO H3373.08, CSIRO H3373.09, CSIRO H3377.01, CSIRO H3736.01, CSIRO H4421.01, CSIRO H4421.02, CSIRO H4686.01, CSIRO H5588.01[b] (G of Carpentaria, QLD, Australia); CSIRO H2376.01, CSIRO H2376.02, CSIRO H2376.03, CSIRO H2376.04 (Cairns, QLD, Australia); CSIRO H38.1 (Papua New Guinea); CSIRO H4913.02 (West Ajkwa River estuary, Irian Jaya, Indonesia); CSIRO H4914.01 (Minajerwi River estuary, Irian Jaya, Indonesia); CSIRO H3305.17 (E of Shelburne Bay, QLD, Australia); CSIRO H3974.01 (Toondah Harbour, QLD, Australia); QM 112946, QM 120793, QM 122355 (Moreton Bay, QLD, Australia).

11. H. uarnacoides.—
BMNH 1867.11.28.210[c] (possible syntype of *Trygon uarnacoides*), BMNH 1892.6.17.15[c] (possible syntype of *Trygon bleekeri*); CAS 213287(1of2), CAS 213287(2of2), CAS 213289 (Thailand); CSIRO H4426.25, CSIRO H4426.26, CSIRO H4426.31[b] (Java, Indonesia); CSIRO H4213.03[b], CSIRO H4919.06[b], CSIRO H4919.07[b], CSIRO H4919.08[b], CSIRO H4921.01, CSIRO H4921.02, CSIRO H4921.03, CSIRO H5479.01[b], CSIRO H5479.16, CSIRO H5479.17, CSIRO H5479.18, CSIRO H5479.19, CSIRO H5481.02, CSIRO H5481.03, CSIRO H5616.01, CSIRO H5616.02, CSIRO H5616.03, CSIRO H5616.04, CSIRO H5616.05, CSIRO H5616.06, SMKK SKN24-4496, UMS MMSK45, UMS MMSK46, UMS MMSK53 (Sandakan, Sabah, Malaysia); CSIRO H5470.01[b,e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H5472.03 (Kuching, Sarawak, Malaysia); MTUF 30000 (India); RMNH 2467[c] (possible syntype of *T. uarnacoides*), RMNH 7441 (Batavia, Indonesia); SMKK KTG112698 (Kinabatangan River, Sabah, Malaysia).

12. H. uarnak.—
BMNH 1953.8.10.15[c] (holotype of *Trygon punctata*) ('East Indian Archipelago'); CAS 213281 (Thailand); CSIRO CA715 (Torres Strait, QLD, Australia); CSIRO H322.1 (Papua New Guinea); CSIRO H1134.1, CSIRO H1134.2, CSIRO H1134.3, CSIRO H1463.3, CSIRO H1920.1, CSIRO H1920.2, CSIRO H1920.3, CSIRO H1920.4, CSIRO H2371.02, CSIRO H2371.03, CSIRO H2371.04, CSIRO H2371.05, CSIRO H4016.01 (WA, Australia); CSIRO H4130.01 (Manila, Philippines); CSIRO H4422.01, CSIRO H4786.01, CSIRO H4786.02, NTM S.11144.001, NTM S.11507.006, NTM S.14869.001[c,e] (G of Carpentaria, QLD, Australia); CSIRO H4542.06 (Kamora Estuary, Irian Jaya, Indonesia); CSIRO H5476.03[b,c,e], CSIRO H5477.01[e], CSIRO H5477.02 (Kota Kinabalu, Sabah, Malaysia); CSIRO H5482.01[e] (Tawau, Sabah, Malaysia); CSIRO H5484.01[e], CSIRO H5617.01 (Semporna, Sabah, Malaysia); RMNH 2459[c] (New Guinea); SMKK KPU5-9196[c] (Kuala Penyu, Sabah, Malaysia); SUML BRU034[c], SUML BRU035[c], SUML BRU111[c], SUML BRU112[c], SUML BRU113[c], SUML BRU114[c], SUML BRU115[c], SUML JPAG035[c], SUML JPAG036[c], SUML JPAG218[c] (Palawan, Philippines).

13. H. undulata.—
CSIRO H5481.01[b,c,e](Sandakan, Sabah, Malaysia); CSIRO H5482.02[a,e], CSIRO H5482.03 (Tawau, Sabah, Malaysia); CSIRO H5483.01[e](Sipitang, Sabah, Malaysia); BMNH 1867.11.28.156[c] (possible syntype) (East Indies); RMNH 7440[c] (possible syntype) (unspecified locality); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

14. H. walga.—
BMNH 89.2.1.4196[c] (possible syntype) (Madras, India); BMNH 1845.3.7.19[c] (paratype of *Trygon nuda*), BMNH 1845.3.7.20[c] (paratype of *Trygon nuda*) (Singapore); BMNH 1867.11.28.158[c] (holotype of *Trygon heterurus*), BMNH 1867.11.28.162[c] (Java, Indonesia); CSIRO H4426.11 (Java, Indonesia); CSIRO H4924.01, CSIRO H4924.02, CSIRO H4924.03, CSIRO H4924.04, CSIRO H4924.05, CSIRO H4924.06, CSIRO H4924.07, CSIRO H4924.08, CSIRO H4924.09, CSIRO H4924.10, CSIRO H4924.11, CSIRO H4924.12, CSIRO H4924.13, CSIRO H4924.14 (Prachuap Khiri Khan, Thailand); CSIRO H4927.04 (Trang, Thailand); CSIRO H5471.04, CSIRO H5471.05, CSIRO H5471.06, CSIRO H5471.07, CSIRO H5474.01[a], CSIRO H5474.02[a], CSIRO H5474.14, CSIRO H5474.15, CSIRO H5474.16, CSIRO H5474.17, CSIRO H5474.18, CSIRO H5474.19, CSIRO H5474.20, CSIRO H5584.07, CSIRO H5584.08, CSIRO H5584.09, UMS MMKK11 (Kota Kinabalu, Sabah, Malaysia); CSIRO H5473.01[e], CSIRO H5473.02[e] (Kudat, Sabah, Malaysia); MNHN 2337[c] (possible syntype) (Red Sea), MNHN 2431[c] (possible syntype)(Ganges Delta, India), MNHN 2438[c] (possible syntype) (Pondicherry, India); MTUF 29998 (Vung Tau, Vietnam); MTUF 29999 (Diamond Harbour, Hooghly River, India).

15a. H. sp. A: Leopard whipray (typical 'leopard' form)—
CAS 213280 (Thailand); CSIRO H635.02, CSIRO H3863.01, CSIRO H3863.02, NTM S.10765.002 (Arafura Sea, NT, Australia); CSIRO H2903.01, CSIRO H3903.02[b] (Gulf of Carpentaria, QLD, Australia); CSIRO H4131.01 (Manila, Philippines); CSIRO H5284.05[e], CSIRO H5478.01[e], UMS MMKK136[e] (Kota Kinabalu, Sabah, Malaysia); CSIRO H5585.02 (off Beruwala, Sri Lanka); RMNH 2473[c] (unspecified locality); SUML BRU084[c] (Philippines); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

15b. H. sp. A: Leopard whipray (atypical 'fine leopard' form)—
CSIRO H5479.08[b,c], UMS MMSK(c4)[e] (Sandakan, Sabah, Malaysia); field photographs of adult specimens[c] (Sabah and Sarawak, Malaysia); uncatalogued LIPI collection[c] (Muara Angke, Jakarta, Indonesia).

15c. H. sp. A: Leopard whipray (var. 'South Africa')—
Sharks Board collection[c] (Natal, South Africa); live Sea World aquarium specimens[c] (Durban, South Africa).

16. H. sp. B: Arabian banded tail —
CSIRO H5700.01[b, c] (South Africa); BPBM 21367[b] (G of Oman, Oman); BPBM 33201(1of2), BPBM 33201(2of2) (Persian G, Kuwait); BPBM 29480 (Persian G, Bahrain); MTUF 20642 (Arabian Sea).

17. H. sp. C: Pakistan whipray —
CAS 29630, CAS 29646 (off Karachi, Pakistan); LACM 38133.048(3of4), LACM 38133.048 (4of4) (Sind, Pakistan); LACM 38311.034 (2of2), LACM 38312.027 (1o2), LACM 38318.011 (3of4), LACM 38318.011 (4of4) (Baluchistan, Pakistan).

18. H. sp. D: Short-tail whipray —
LACM 38130.047(1of3), LACM 38130.047(2of3), LACM 38130.047(3of3) (Sind, Pakistan); LACM 38131.043 (Karachi, Pakistan); MTUF 30005[?] (Farakka, India); CAS 141048[?] (Chandpur, Megna River, Bangladesh).

19. H. sp. E: Hortles whipray —
CSIRO H4549.02, CSIRO H4915.01[e], CSIRO H4916.01, CSIRO H5285.01 (Ajkwa River estuary Irian Jaya, Indonesia); CSIRO H5155.01[a,e] (Minajerwi River estuary, Irian Jaya, Indonesia); CSIRO H4917.01 (Poriri Island, Irian Jaya, Indonesia).

20. H. sp. F: Tube-mouth whipray —
CSIRO H5472.01[e], CSIRO H5485.01 (Kuching, Sarawak, Malaysia).

21. H. sp. G: Cooks whipray —
MTUF 30001[e] (Chao Phraya River, Nakhonsawan, Thailand).

Non-*Himantura* Indo-Pacific stingrays
1. Dasyatis acutirostra.—
HUMZ 107588 (paratype), HUMZ 107591 (paratype) (Japan).

2. D. kuhlii.—
CSIRO CA4307 (north west of WA, Australia); CSIRO H4122.03 (Sri Lanka); CSIRO H4926.01 (Nakhon Si Thammarat market, Thailand); CSIRO H5590.01[a] (G of Carpentaria, QLD, Australia).

3. D. laosensis.—
MTUF 30207, MTUF 30208 (Mekong River, Vietnam).

4. D. leylandii.—
CSIRO H3332.02 (Gulf of Carpentaria, W of Weipa, Qld); CSIRO H3361.07[a], CSIRO H5590.02[a] (G of Carpentaria, NT, Australia).

5. D. violacea.—
CSIRO H311.01 (W of Coffin Bay, Great Australian Bight, SA); CSIRO T450[a] (Australia).

6. D. zugei.—
CAS 54592(1o3), CAS 54592(2o3), CAS 54592(3o3) (Taiwan); CSIRO H4426.05, CSIRO H4426.06, CSIRO H4426.07, CSIRO H4426.09, CSIRO H4426.10 (Java, Indonesia); CSIRO H4924.20[a] (Prachuap Khiri Khan, Thailand); CSIRO H5471.03, CSIRO H5475.02[b] (Kota Kinabalu, Sabah, Malaysia).

7. Pastinachus sephen.—
CSIRO CA4048 (NW of Port Hedland, WA, Australia); CSIRO H4122.04 (off Beruwala, Sri Lanka); CSIRO H5479.20[b], CSIRO H5480.03[a] (Sandakan, Sabah, Malaysia).

8. Pastinachus sp. .—
CSIRO H4426.27 (Muara Angke Market, Jakarta, Indonesia); CSIRO H5472.02 (Kuching, Sarawak, Malaysia).

OUTGROUP
1. Amphi-American *Himantura pacifica.—*
ROM ICH66838[a,c] (Atlantic Ocean beach, Guyana).

2. Amphi-American *H. schmardae.—*
ROM ICH66845[a, c] (Playa Panama, Costa Rica).

3. Plesiobatis daviesi.—
CSIRO CA4238 (SW of Rowley Shoals, WA, Australia); CSIRO H832.1 (South of Marion Reef, Marian Plateau, QLD, Australia).

4. Rhinobatos typus.—
CSIRO H3737.01 (beach near Weipa, QLD, Australia); NTM S.10002.005 (west side of Cape Thouin, Mundabullangana Beach, WA, Australia; 20° 22' S 118 ° 06' E); NTM S.11507.005 (Ludmilla Creek, Darwin, NT, Australia; 12 ° 25' S 130 ° 50' E).

Additional comparative materials
1. D. fluviorum.—
CSIRO H5286.01[a] (Kamora River estuary, Irian Jaya, Indonesia).

2. D. longus.—
LACM 49779-3[a] (off Clarion Island, Mexico).

APPENDIX 3.1.1. Materials examined for phylogenetic analyses. Listing follows species name (in alphabetical order), specimen registration number or identification tag (for uncatalogued specimens) in alphabetical order (see Chapter 2 for museum and institutional codes), and locality by country (details given where appropriate). [a]partially dissected, [b]skeletal part only, [c]photograph only, [d]radiograph only, [e]genetically analyzed (see also Chapter 4, Appendix 4.1.1). Type specimens are indicated. [East Indies — name formerly applied to southeastern Asia, embracing the Indian subcontinent].

INGROUP

Indo-Pacific *Himantura*

1. H. chaophraya.—
CSIRO H2503.01[a] (Pentecost River, WA, Australia);
CSIRO H5283.01[a], SMKK KTG2-23397, SMKK KTG3-20497, SMKK KTG7-21096, UMS MMKG1 (Kinabatangan River, Sabah, Malaysia);
MTUF 30203[e] (Bhagalpur, India);
MTUF 30204[e], MTUF 30205, MTUF 30206 (Chao Phraya River, Thailand);
SMKK BFT1-697[e] (Padas River, Sabah, Malaysia);
SMKK SKN10-15697[e] (Sandakan, Sabah, Malaysia).

2. H. fai.—
CSIRO H687.2, CSIRO H1910.1, CSIRO H5671.01 (NW Shelf, WA, Australia);
CSIRO H2753.01, CSIRO H2754.01, CSIRO H2756.01 (Heron Island, QLD, Australia);
CSIRO H3355.01, CSIRO H3378.01, CSIRO H5207.01[a,e] (G of Carpentaria, QLD, Australia);
CSIRO H4426.33[b] (Java, Indonesia);
CSIRO H5480.01[b,e] (Sandakan, Sabah, Malaysia);
USNM 51712[c,d] (holotype)(Apia, Samoa).

3a. H. gerrardi: var 'small denticle'—
BMNH 1843.5.19.1[c] (syntype of *T. gerrardi* Gray 1851), BMNH 1846.11.18.49[c] (syntype of *T. gerrardi* Gray 1851), BMNH 1867.11.28.160[c] (India);
CSIRO H4919.01, CSIRO H4919.03, CSIRO H5479.04, CSIRO H5479.09, CSIRO H5479.10, SMKK SKN22-4496, UMS MMSK35[e], UMS MMSK36[e], UMS MMSK37[e], UMS MMSK38 (Sandakan, Sabah, Malaysia);
CSIRO H4122.01, CSIRO H4122.02, CSIRO H4123.01 (off Beruwala, Sri Lanka);
CSIRO H4426.20, CSIRO H4426.21, CSIRO H4426.22, CSIRO H4426.23, CSIRO H4426.24 (Java, Indonesia);
CSIRO H4922.01, CSIRO H4922.02, CSIRO H4922.03, CSIRO H5284.01, CSIRO H5284.02, CSIRO H5284.03[a], CSIRO H5284.04[b], CSIRO H5474.03, CSIRO H5474.04, CSIRO H5474.05, CSIRO H5474.06, CSIRO H5474.07, CSIRO H5474.08, CSIRO H5474.09, CSIRO H5474.10, CSIRO H5474.11, CSIRO H5474.12, CSIRO H5474.13, CSIRO H5476.01[e], CSIRO H5476.02[e], CSIRO H5476.04, CSIRO H5476.05, CSIRO H5476.06, CSIRO H5476.07, CSIRO H5584.01, CSIRO H5584.02, CSIRO H5584.03, CSIRO H5584.04, CSIRO H5584.05, CSIRO H5584.06, CSIRO H5584.10, CSIRO H5612.01, UMS MMKK24[e] (Kota Kinabalu, Sabah, Malaysia);
CSIRO H4926.09, CSIRO H4926.10 (Nakhon Si Thammarat, Thailand);
CSIRO H4927.05, H4927.07 (Trang, Thailand);
MTUF 30004 (Thailand);
NMV A949 (possible syntype) (Indonesia).

3b. H. gerrardi: var 'large denticle'—
CSIRO H4919.02, CSIRO H5479.05, CSIRO H5479.06, CSIRO H5479.07, CSIRO H5479.11, (Sandakan, Sabah, Malaysia);
CSIRO H4918.02[a], CSIRO H5482.04, CSIRO H5482.05, UMS MMT1[e], UMS MMT5 (Tawau, Sabah, Malaysia);
CSIRO H5484.02, CSIRO H5484.03, CSIRO H5484.04, CSIRO H5484.05, CSIRO H5484.06, CSIRO H5484.07, CSIRO H5617.02, CSIRO H5617.03, CSIRO H5617.04, CSIRO H5617.05 (Semporna, Sabah, Malaysia).

4. H. granulata.—

AMS I9763 (holotype) (New Guinea);
CAS 152032 (Palau);
CSIRO CA1255 (N of Anson Bay, WA, Australia);
CSIRO H962.1, NTM S10718.062 (NT, Australia);
CSIRO H2751.01 (Groote Eylandt, NT, Australia);
CSIRO H3864.01 (E of Cape York Peninsula, QLD, Australia);
CSIRO H4417.01 (NE of Shelburne Bay, QLD, Australia);
CSIRO H4426.32[a] (Java, Indonesia);
MTUF26700, MTUF26703, MTUF26719, MTUF26903[c], MTUF26906 (Micronesia);
QM I5879, QM I20184 (QLD, Australia);
SMF 4747[d] (Maldives);
SUML JPAG207 (Philippines).

5. H. imbricata.—
BPBM 33199(1of2), BPBM 33199(2of2) (Kuwait);
CAS 141045 (mouth of Ganges River, India);
LACM 38129-83(1of3), LACM 38129-83(2of3), LACM 38129-83(3of3), LACM 38130-60(1of10), LACM 38130-60(2of10), LACM 38130-60(3of10), LACM 38130-60(4of10), LACM 38314-24, LACM 38134-37(1of2) (Pakistan);
NTM S13160.009 (Sri Lanka).

6. H. jenkinsii.—
CAS 213283, CAS 213284, CAS 213286(1of3), CAS 213286(2of3) (Thailand);
CSIRO CA3947, CSIRO H4004.05[b] (NW shelf, WA, Australia);
CSIRO H2906.01[a] (Arafura Sea, NT, Australia);
CSIRO H3375.01, CSIRO H3622.01[a], CSIRO H3649.01(G of Carpentaria);
CSIRO H4123.02 (Sri Lanka); CSIRO H4918.01 (Tawau, Sabah, Malaysia);
CSIRO H5475.01[a,c] (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5585.01[b] (off Beruwela, Sri Lanka);
SUML BRU116, SUML JPAG213[c] (Philippines).

7. H. oxyrhyncha.—
MTUF 30002 (Thailand);
ZRC 42984[a], ZRC 42991, ZRC 42992[c] (Kapuas Basin, Kalimantan, Indonesia).

8. H. pastinacoides.—
BMNH 1867.11.28.161[c] (designated as type specimen by BMNH) ('Far East Indies');
CAS 213285 (Thailand);
CSIRO H4424.01, CSIRO H4424.02, CSIRO H4424.03, CSIRO H5613.01[b,c] (Kuching, Sarawak, Malaysia);
CSIRO H4426.01 (Java, Indonesia);
CSIRO H5471.01[c] (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5479.02[b,c],
CSIRO H5479.03, CSIRO H5479.12, CSIRO H5479.13, CSIRO H5479.14, CSIRO H5479.15, CSIRO H5480.02, CSIRO H5614.01[b,c], CSIRO H5615.01, CSIRO H5615.02, UMS MMSK7, UMS MMSK39, UMS MMSK40 (Sandakan, Sabah, Malaysia);
CSIRO H5618.01 (Semporna, Sabah, Malaysia);
NMV A914 (possible syntype) (Indonesia).

9. H. signifer.—
ZRC 42547[a,c] (Mekong Basin, Thailand);
ZRC 42647[c], ZRC 42648[c] (Batang Hari, Sumatra, Thailand);
ZRC 42993, ZRC 42984 (Kapuas Basin, Kalimantan, Indonesia).

10. H. toshi.—
AMS IA.39 (holotype) (Clarence River estuary, NSW, Australia);
CSIRO CA2405, CSIRO CA2406, CSIRO CA4271, CSIRO H312.1, CSIRO H635.1, CSIRO H635.03, CSIRO H635.04, CSIRO H959.1, CSIRO H959.2, CSIRO H959.4, CSIRO H963.1, CSIRO H963.2, CSIRO H963.3, CSIRO H964.1, CSIRO H964.2, CSIRO H3380.01, CSIRO H3380.02, CSIRO H3381.01, CSIRO H3381.02, CSIRO H3381.03, CSIRO H3383.01, CSIRO H3387.01[c], CSIRO H3387.02, CSIRO H3387.03, CSIRO H5204.01, CSIRO H5205.01, CSIRO H5206.01, CSIRO H5586.01, CSIRO H5586.02[b], CSIRO H5586.03[b], CSIRO H5586.04[b], CSIRO H5589.01[b], CSIRO T698, CSIRO T699, CSIRO T700, NTM S12416.001 (NT, Australia);
CSIRO CA1245, CSIRO CA3994, CSIRO H1034.1, CSIRO H1034.2, CSIRO H1464.4, CSIRO H5587.01[b], CSIRO H1041.02, CSIRO H4077.01, CSIRO H4077.02, CSIRO H4077.03, CSIRO H4077.04, CSIRO H4083.01, WAM P29180.001 (NW Shelf, WA, Australia);
CSIRO H38.1 (Papua New Guinea);
CSIRO H1220.2, CSIRO H1220.01[a], CSIRO H1222.1[a], CSIRO H1222.2, CSIRO H3322.02, CSIRO H3329.01, CSIRO H3352.01[c], CSIRO H3369.01, CSIRO H3373.01, CSIRO H3373.02, CSIRO H3373.03, CSIRO H3373.08, CSIRO H3373.09, CSIRO H3377.01, CSIRO H3736.01, CSIRO H4421.01, CSIRO H4421.02, CSIRO H4686.01, CSIRO H5588.01[b] (G of Carpentaria, QLD, Australia);
CSIRO H2376.01, CSIRO H2376.02, CSIRO H2376.03, CSIRO H2376.04 (Cairns, QLD, Australia);
CSIRO H4913.02 (West Ajkwa River estuary, Irian Jaya, Indonesia);
CSIRO H4914.01 (Minajerwi River estuary, Irian Jaya, Indonesia);
CSIRO H3305.17 (E of Shelburne Bay, QLD, Australia);
CSIRO H3974.01 (Toondah Harbour, QLD, Australia);
QM I12946, QM I20793, QM I22355 (Moreton Bay, QLD, Australia).

11. H. uarnacoides.—
CAS 213287(1of2), CAS 213287(2of2), CAS 213289 (Thailand);
H4426.25, H4426.26, CSIRO H4426.31[b] (Java, Indonesia);
CSIRO H4213.03[b], CSIRO H4919.06[b], CSIRO H4919.07[b], CSIRO H4919.08[b], H4921.01, H4921.02, H4921.03, CSIRO H5479.01[b], CSIRO H5479.16, CSIRO H5479.17, CSIRO H5479.18, CSIRO H5479.19, CSIRO H5481.02, CSIRO H5481.03, CSIRO H5616.01, CSIRO H5616.02, CSIRO H5616.03, CSIRO H5616.04, CSIRO H5616.05, CSIRO H5616.06, UMS MMSK45, UMS MMSK46, UMS MMSK53 (Sandakan, Sabah, Malaysia);
CSIRO H5470.01[b,e] (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5472.03 (Kuching, Sarawak, Malaysia);
MTUF 30000 (India);
SMKK KTG112698 (Kinabatangan River, Sabah, Malaysia).

12. H. uarnak.—
CAS 213281 (Thailand);
CSIRO CA715 (Torres Strait, QLD, Australia);
CSIRO H322.1 (Papua New Guinea);
CSIRO H1134.1, CSIRO H1134.2, CSIRO H1134.3, CSIRO H1463.3, CSIRO H1920.1, CSIRO H1920.2, CSIRO H1920.3, CSIRO H1920.4, CSIRO H2371.02, CSIRO H2371.03, CSIRO H2371.04, CSIRO H2371.05, CSIRO H3863.01, CSIRO H3863.02, CSIRO H4016.01 (WA, Australia);
CSIRO H4130.01, CSIRO H4131.01 (Manila, Philippines);
CSIRO H4422.01, CSIRO H4786.01, CSIRO H4786.02, NTM S11144.001, NTM S11507.006, NTM S14869.001[e] (G of Carpentaria, QLD, Australia);
CSIRO H4542.06 (Kamora Estuary, Irian Jaya, Indonesia).
CSIRO H5476.03[b,c,e], CSIRO H5477.01[e], CSIRO H5477.02 (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5482.01[e] (Sabah: Tawau);
CSIRO H5484.01[c], CSIRO H5617.01 (Semporna, Sabah, Malaysia);
SUML BRU112[c], SUML BRU115[c] (Palawan, Philippines).

13. H. undulata.—
CSIRO H5481.01[b,c,e] (Sandakan, Sabah, Malaysia);
CSIRO H5482.02[a,e], CSIRO H5482.03 (Tawau, Sabah, Malaysia);
CSIRO H5483.01[e] (Sipitang, Sabah, Malaysia);
BMNH 1867.11.28.156[c] (East Indies).

14. H. walga.—
CSIRO H4426.11 (Java, Indonesia);
CSIRO H4924.01, CSIRO H4924.02, CSIRO H4924.03, CSIRO H4924.04, CSIRO H4924.05, CSIRO H4924.06, CSIRO H4924.07, CSIRO H4924.08, CSIRO H4924.09, CSIRO H4924.10, CSIRO H4924.11, CSIRO H4924.12, CSIRO H4924.13, CSIRO H4924.14 (Prachuap Khiri Khan, Thailand);
CSIRO H4927.04 (Trang, Thailand);
CSIRO H5471.04, CSIRO H5471.05, CSIRO H5471.06, CSIRO H5471.07, CSIRO H5474.01[a], CSIRO H5474.02[a], CSIRO H5474.14, CSIRO H5474.15, CSIRO H5474.16, CSIRO H5474.17, CSIRO H5474.18, CSIRO H5474.19, CSIRO H5474.20, CSIRO H5584.07, CSIRO H5584.08, CSIRO H5584.09, UMS MMKK11 (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5473.01[e], CSIRO H5473.02[e] (Kudat, Sabah, Malaysia);
MTUF 29998 (Vung Tau, Vietnam);
MTUF 29999 (Diamond Harbour, Hooghly River, India).

15a. H. sp. A: Leopard whipray (typical 'leopard' form)—
CAS 213280 (Thailand);
CSIRO H635.02, CSIRO H3863.01, CSIRO H3863.02 (Arafura Sea, NT, Australia);
CSIRO H2903.01, CSIRO H3903.02[b] (G of Carpentaria, QLD, Australia);
CSIRO H4131.01 (Manila, Philippines);
CSIRO H5284.05[e], CSIRO H5478.01[e], UMS MMKK136[e] (Kota Kinabalu, Sabah, Malaysia);
CSIRO H5585.02 (off Beruwala, Sri Lanka);
SUML BRU084[c] (Philippines).

15b. H. sp. A: Leopard whipray (atypical 'fine leopard' form)—
CSIRO H5479.08[b,c], UMS MMSK(c4)[e] (Sandakan, Sabah, Malaysia);
field photographs of adult specimens[c] (Sabah and Sarawak, Malaysia);
uncatalogued LIPI collection[c] (Java, Indonesia).

15c. H. sp. A: Leopard whipray (var. 'South Africa')—
Sharks Board collection[c] (Natal, South Africa);
live Sea World aquarium specimens[c] (Durban, South Africa);
Wallace 1967:44, figure 22;
Van der Elst 1988 (on habitat quoted by Whitfield 1998);
Whitfield 1998:55, figure, distribution map.

16. H. sp. B: Arabian banded tail —
CSIRO H5700.01[b, c] (South Africa);
BPBM 21367[b] (G of Oman, Oman);
BPBM 33201(1of2), BPBM 33201(2of2) (Persian G, Kuwait);
BPBM 29480 (Persian G, Bahrain);
MTUF 20642 (Arabian Sea).

17. H. sp. C: Pakistan whipray —
CAS 29630, CAS 29646 (off Karachi, Pakistan);
LACM 38133.048 (3of4), LACM 38133.048 (4of4) (Sind, Pakistan);
LACM 38311.034 (2of2), LACM 38312.027 (1o2), LACM 38318.011 (3of4), LACM 38318.011 (4of4) (Baluchistan, Pakistan).

18. H. sp. D: Short-tail whipray —
LACM 38130.047 (1of3), LACM 38130.047 (2of3), LACM 38130.047 (3of3) (Sind, Pakistan);
LACM 38131.043 (Karachi, Pakistan).

19. H. sp. E: Hortles whipray —
CSIRO H4549.02 (paratype), CSIRO H4915.01[e] (paratype), CSIRO H4916.01 (paratype), CSIRO H5285.01 (paratype) (Ajkwa River estuary Irian Jaya, Indonesia);
CSIRO H5155.01[a,e] (holotype) (Minajerwi River estuary, Irian Jaya, Indonesia);
CSIRO H4917.01 (Poriri Island, Irian Jaya, Indonesia).

20. H. sp. F: Tube-mouth whipray —
CSIRO H5472.01[e] (paratype), CSIRO H5485.01 (holotype) (Kuching, Sarawak, Malaysia).

21. H. sp. G: Cooks whipray —
MTUF 30001 (holotype) (Chao Phraya River, Nakhonsawan, Thailand).

Non-*Himantura* Indo-Pacific stingrays

1. Dasyatis acutirostra.—
HUMZ 107588 (paratype) , HUMZ 107591 (paratype) (Japan).

2. D. kuhlii.—
CSIRO CA4307 (north west of WA, Australia); CSIRO H4122.03 (Sri Lanka); CSIRO H4926.01 (Nakhon Si Thammarat market, Thailand); CSIRO H5590.01[a] (G of Carpentaria, QLD, Australia).

3. D. laosensis.—
MTUF 30207, MTUF 30208 (Mekong River, Vietnam).

4. D. leylandii.—
CSIRO H3332.02 (Gulf of Carpentaria, W of Weipa, Qld); CSIRO H3361.07[a], CSIRO H5590.02[a] (G of Carpentaria, NT, Australia).

5. D. violacea.—
CSIRO H311.01 (W of Coffin Bay, Great Australian Bight, SA); CSIRO T450[a] (Australia).

6. D. zugei.—
CAS 54592(1o3), CAS 54592(2o3), CAS 54592(3o3) (Taiwan); CSIRO H4426.05, CSIRO H4426.06, CSIRO H4426.07, CSIRO H4426.09, CSIRO H4426.10 (Java, Indonesia); CSIRO H4924.20[a] (Prachuap Khiri Khan, Thailand); CSIRO H5471.03, CSIRO H5475.02[b] (Kota Kinabalu, Sabah, Malaysia).

7. Pastinachus sephen.—
CSIRO CA4048 (NW of Port Hedland, WA, Australia); CSIRO H4122.04 (off Beruwala, Sri Lanka); CSIRO H5479.20[b], CSIRO H5480.03[a] (Sandakan, Sabah, Malaysia).

8. Pastinachus sp.—
CSIRO H4426.27 (Muara Angke Market, Jakarta, Indonesia); CSIRO H5472.02 (Kuching, Sarawak, Malaysia).

OUTGROUP

1. Amphi-American *Himantura pacifica.—*
ROM ICH66838[a,c] (Atlantic Ocean beach, Guyana).

2. Amphi-American *H. schmardae.—*
ROM ICH66845[a,c] (Playa Panama, Costa Rica).

3. Plesiobatis daviesi.—
CSIRO CA4238 (SW of Rowley Shoals, WA, Australia); CSIRO H832.1 (S of Marion Reef, Marian Plateau, QLD, Australia).

4. Rhinobatos typus.—
CSIRO H3737.01 (beach near Weipa, QLD, Australia); NTM S10002.005 (west side of Cape Thouin, Mundabullangana Beach, WA, Australia; 20° 22' S 118° 06' E); NTM S11507.005 (Ludmilla Creek, Darwin, NT, Australia; 12° 25' S 130° 50' E).

Additional comparative materials

1. D. fluviorum.—
CSIRO H5286.01[a] (Kamora River estuary, Irian Jaya, Indonesia).

2. D. longus.—
LACM 49779-3[a] (off Clarion Island, Mexico).

APPENDIX 3.2.1. List of characters and their states coded for the matrix in Appendix 3.2.2.

1. Snout apex: 0 = angular, 1= not angular.
2. Apices of pectoral-fins: 0 = acutely angular, 1 = moderately angular, 2 = not angular, or obtusely angular.
3. Free rear tips of pectoral-fins: 0 = angular, 1 = rounded.
4. Orbits: 0 = protruded or clearly demarcated from head, 1 = embedded in head.
5. Spiracle, position on head: 0 = dorsolateral, 1 = lateral or vertically positioned.
6. Anterior margin vs. free posterior margin of nasal curtain: 0 = wider, 1 = narrower.
7. Free posterior margin of nasal curtain: 0 = not reaching to lower jaw, 1 = reaching lower jaw.
8. Nostril, shape: 0 = circular, 1 = slit-like.
9. Nostril, posterior end: 0 = flared, 1 = not flared.
10. Medial indentation of lower jaw: 0 = absent or only with weak concavity, 1 = present.
11. Oral papillae: 0 = absent, 1 = present.
12. Pelvic-fins: 0 = free rear tip posterior to apex, 1 = free rear tip level or anterior to apex.
13. Clasper of mature males: 0 = tip rounded or bluntly pointed appearing rod-like, 1 = tip pointed appearing spatulate.
14. Clasper, pseudosiphon: 0 = pseudosiphon absent, 1 = pseudosiphon present, positioned on anterior of hypopyle near clasper groove, 2 = pseudosiphon present, positioned on inner margin of clasper.
15. Clasper, pseudorhipidion: 0 = present, 1 = absent.
16. Cross section of tail base: 0 = depressed, 1 = circular.
17. Cross section of tail at sting base: 0 = constricted, 1 = not constricted.
18. Tail dorsal fold: 0 = present, 1 = absent or rudimentary.
19. Tail ventral fold: 0 = present, 1 = absent or rudimentary.
20. Secondary denticle band in sub-adults and adults: 0 = absent, 1 = present.
21. Tertiary denticle band: 0 = absent, 1 = present.
22. Enlarged mid-scapular denticles in young and adults: 0 = absent, 1 = present.
23. Enlarged row of denticles along trunk to midline of tail in sub-adults and adults: 0 = absent, 1 = present.
24. Infra-orbital loop: 0 = simple, not reticulated, 1 = extensive reticulation and looping.
25. Infra-orbital loop: 0 = anterior or slightly posterior to the first gill slit, 1 = extending to between first and fifth gill slit, 2 = extending beyond fifth gill slit.
26. Lateral hook formed by subpleural component of hyomandibular canal: 0 = absent (broadly rounded), 1 = shallow, 2 = deeply indented.
27. Lateral hook formed by jugular component of hyomandibular canal: 0 = shallow (broadly rounded), 1 = deep.
28. Anterior profile of neurocranium: 0 = strongly double convex, 1 = anterolaterally angular.
29. Preorbital process: 0 = short (knob-like), 1 = moderately elongate (rod-like), 2 = extremely elongate (twig-like).
30. Position of anterior foramen for preorbital canal: 0 = approximately level or forwards of anterior margin of dorsal fontanelle, 1 = markedly posterior of anterior margin of dorsal fontanelle.
31. Mid-region of dorsal fontanelle: 0 = greatly constricted, 1 = moderately constricted.
32. Supra-orbital crest: 0 = reduced to a keel along the dorsolateral margin of the orbital region, 1 = plate-like.
33. Margin of sphenopterotic ridge in dorsal view: 0 = angular, 1 = broadly rounded.
34. Process on sphenopterotic ridge: 0 = absent, 1 = present.
35. Angular cartilage between mandibular and hyomandibular cartilages: 0 = absent, 1 = present.
36. First segmentation of the propterygium: 0 = along nasal capsule; 1 = at or anterior of nasal capsule.
37. Scapulocoracoid height in lateral face: 0 = equal to or shorter than wide, 1 = taller than wide.
38. Puboischiadic bar: 0 = angularly arched, 1 = not angularly arched.
39. Median prepelvic process: 0 = present, 1 = absent.
40. Anterolateral processes: 0=present, 1=absent.
41. Shape, terminal tip of axial cartilage of the mixopterygium: 0 = short, spatula-like, 1 = elongated, tip pointed.
42. Diplospondylous vertebrae: 0 = extended to or slightly beyond sting base (0-10 centra), 1 = not extended to sting base.
43. Cartilaginous radials of caudal fin or caudal folds: 0 = present or only as remnants, 1 = absent (caudal fin and/or fold entirely absent).
44. Disc dorsal patterning: 0 = absent, 1 = present.
45. Tail banding: 0 = present, 1 = absent.
46. Sexual dental dimorphism: 0 = present, 1 = absent.
47. Habitat distribution: 0 = obligate freshwater, 1 = brackishwater, 2 = marine.

APPENDIX 3.2.2. Character matrix of 31 species of whip-tailed stingrays. Included in the analysis are two forms of *H. gerrardi* (a- small denticle, b- large denticle). '?' indicate unknown state or missing data; '&' and '$' indicate polymorphic states (0,1 and 1,2 respectively).

		1	11111	11112	22222	22223	33333	33334	44444	44
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67
H. chaophraya	12101	11101	11021	11111	11012	01101	11010	&0101	?1101	1&
H. fai	01101	11101	11021	11111	10012	21111	01010	01101	01101	12
H. gerrardi(a)	01101	11101	11021	11111	?1010	21110	11010	00111	?11&0	12
H. gerrardi(b)	01101	11101	11021	11111	?1010	21110	1?010	0?111	?1110	12
H. granulata	02101	11101	&1021	00111	1&011	01000	01010	01111	001&1	1$
H. imbricata	02100	1110&	11021	00111	0&1??	??011	1?01&	0?111	?0101	0&
H. jenkinsii	01101	11101	11021	11111	01111	11110	01010	00111	11101	12
H. oxyrhyncha	02101	11101	11???	11111	11111	01111	11010	00101	?0111	00
H. pastinacoides	0$101	11101	11021	01111	01011	11110	1101&	00111	11101	1$
H. signifer	02100	11101	11021	00111	11111	01011	11110	00101	10101	00
H. toshi	0&101	11101	11021	11111	01010	21110	11010	00111	111&0	1$
H. uarnacoides	01101	11101	11021	01111	01012	21110	11010	00111	11101	1$
H. uarnak	0$101	11101	11021	11111	11011	21110	11010	00111	11110	12
H. undulata	01101	11101	11021	11111	11&11	11110	11010	00111	11110	12
H. walga	02100	11101	11021	00111	0&100	21011	1110&	00111	10101	0&
H. sp. A	01101	11101	11021	11111	11011	21110	11010	00111	01110	12
H. sp. B	01101	11101	11?21	11111	?101?	??110	1?010	0?111	?110&	12
H. sp. C	01101	11101	11?21	11111	?101?	??110	1?010	0?111	?1100	12
H. sp. D	01101	11101	11?21	11111	?101?	??110	1?010	0?111	?1101	12
H. sp. E	02101	11101	01021	01111	01012	11101	11100	10101	11101	11
H. sp. F	02101	11101	01???	01111	01011	11101	11001	00110	???01	11
H. sp. G	02101	11100	11021	00111	1111?	??011	11010	0?111	?0101	00
D. acutirostra	01101	00010	01?0?	11110	0011?	?????	?????	?????	??101	02
D. kuhlii	00001	11111	11110	01000	00100	11021	0000&	00000	10010	02
D. laosensis	01101	11101	10?0?	01000	001??	?????	?????	?????	??101	00
D. leylandii	00101	11111	11110	01000	00100	10021	00000	00000	10110	02
D. violacea	10011	10011	10000	10100	00100	01011	01000	11100	?0001	12
D. zugei	01110	01010	0100?	10100	00100	20111	1110&	10111	?0101	01
P. sephen	01101	11100	11???	00101	01&00	20011	11011	01001	10101	?$
P. sp.	01101	11100	11???	00101	01&??	??011	11011	?1001	10101	?1
H. pacifica	02101	11111	10???	01111	?1000	00021	0?001	0?001	?0101	?2
H. schmardae	12101	11111	10???	01111	11000	0?021	0?001	0?001	?0101	?2

Appendix 4.1.1. List in alphabetical order of tissue samples used in this study, and the gene sequenced (16S, cyt. *b*). Samples were preserved in 90% ethanol, unless otherwise indicated. Numbers after species name are used to distinguish samples of the same species. Question marks before species name indicates specimens whose identity could not be verified (see Results).

Species	Sample code	Specimen Registration Number	Locality	Collector	Year collected	16S	cyt. *b*
Indo-Pacific *Himantura*							
H. chaophraya 1	SR99	SMKK SKN10-15697	Malaysia (Kinabatangan, Sabah)	S. Mycock & R. Cavanagh	1997	+	+
H. chaophraya 2	SR105	SMKK BFT1- 697	Malaysia (Padas River, Sabah)	S. Mycock & R. Cavanagh	1997	+	+
H. chaophraya 3	DWPL1a	-specimen not saved-	Australia (Daley River, Northern Territory)	D. Wilson	1999	+	+
H. chaophraya 4	HC1	-specimen not saved-	Australia (Daley River, Northern Territory)	P. Last	1999	+	+
H. chaophraya 5	J3	MTUF [India-5]	India (Ganges River)	H. Ishihara	2000	+	
H. chaophraya 6	J5	MTUF [T-3]	Thailand (Chaophraya River)	H. Ishihara	2000	+	+
H. fai 1	(60)	CSIRO H5207.01	Australia (north Groote Eylandt, G.Carpentaria)	B.M.M	1998	+	
H. fai 2	HF82	CSIRO H5480.01	Malaysia (Sandakan, Sabah)	B.M.M	1999		+
H. gerrardi 1	(50)	UMS MMSK36	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. gerrardi 2	(52)	UMS MMSK37	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	
H. gerrardi 3	(5)	CSIRO H5476.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
H. gerrardi 4	(11)	UMS MMKK24	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
H. gerrardi 5	(49)	UMS MMSK35	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. gerrardi 6	(7)	CSIRO H5476.02	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
?*H. gerrardi* 7	(23)	UMS MMT1	Malaysia (Tawau, Sabah)	B.M.M	1999	+	
?*H. gerrardi* 8	(108)	- specimen not saved-	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
?*H. gerrardi* 9	MMPL7	- specimen not saved-	India (Cochin)	P. Last	1999	+	
?*H. gerrardi* 10	MMPL8	- specimen not saved-	India (Cochin)	P. Last	1999	+	
H. granulata 1	(124)	- specimen not saved; photo only-	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. granulata 2	(125)	- specimen not saved; photo only-	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. granulata 3	J1	MTUF 26903	Pohnpei	H. Ishihara	2000	+	+
H. imbricata	MMPL2	- specimen not saved-	India (Cochin)	P. Last	1999	+	+
H. jenkinsii 1	(22)	CSIRO H5475.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
H. jenkinsii 2	BRU109	- specimen not saved-	Philippines	^SUML-WWF personnel	2000	+	
H. jenkinsii 3	JPAG213	SUML JPAG213	Philippines (Palawan)	^SUML-WWF personnel	2000	+	
H. oxyrhyncha	NUS10	ZRC 42992	Indonesia (Kapuas)[a]	K. Lim & H.H.Tan	1998	+	+
H. pastinacoides	(62)	CSIRO H5471.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. signifer 1	NUS1	ZRC 42647	Indonesia (Sumatera)[a]	K. Lim & H.H.Tan	1998	+	
H. signifer 2	NUS4	ZRC 42648	Indonesia (Sumatera)[a]	K. Lim & H.H.Tan	1998	+	+
H. signifer 3	NUS3	ZRC 42547	Thailand (Mekong)[a]	K. Lim & H.H.Tan	1998	+	+

continued...

Appendix 4.1.1. continued

Species	Sample code	Specimen Registration Number	Locality	Collector	Year collected	16S	cyt. *b*
H. toshi 1	GY1	CSIRO H3387.01	Australia (Queensland)[c]	G. Yearsley	1997	+	+
H. toshi 2	GY2	CSIRO H3352.01	Australia (nw of Prince of Wales Island, Qld)[c]	G. Yearsley	1997	+	+
H. toshi 3	M7	- specimen not saved-	Australia (Gulf of Carpentaria)[c]	B.M.M	1998		+
H. uarnacoides 1	(20)	CSIRO H5470.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. uarnacoides 2	(126)	- specimen not saved-	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	
H. uarnak 1	(2)	CSIRO H5476.03	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. uarnak 2	(72)	CSIRO H5477.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. uarnak 3	(89)	CSIRO H5484.01	Malaysia (Semporna, Sabah)	B.M.M	1999	+	+
H. uarnak 4	BRU111	- specimen not saved-	Philippines (Palawan)	^SUML-WWF personnel	2000	+	
H. uarnak 5	(29)	CSIRO H5482.01	Malaysia (Tawau, Sabah)	B.M.M	1999	+	
H. uarnak 6	EM330	- specimen not saved-	Papua New Guinea	P. Kailola	1999	+	+
H. uarnak 7	MMPK3	- specimen saved, not located-	Indonesia (Irian Jaya)	P. Kailola	1999	+	
H. uarnak 8	MMPK7	- specimen saved, not located-	Indonesia (Irian Jaya)	P. Kailola	1999	+	+
H. uarnak 9	NTM1b	NTM S14869.001	Australia (near Darwin)	G. Dally	1999	+	
H. undulata 1	(27)	CSIRO H5482.02	Malaysia (Tawau, Sabah)	B.M.M	1999	+	
H. undulata 2	(74)	CSIRO H5483.01	Malaysia (Sipitang, Sabah)	B.M.M	1999	+	+
H. undulata 3	(86)	CSIRO H5481.01	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. walga 1	(15)	CSIRO H5473.02	Malaysia (Kudat, Sabah)	B.M.M	1999	+	+
H. walga 2	(17)	CSIRO H5473.01	Malaysia (Kudat, Sabah)	B.M.M	1999	+	
H. sp. A 1	(3)	- specimen not saved; photo only-	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. sp. A 2	(59)	UMS MMSK(c4)	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	+
H. sp. A 3	(84)	- specimen not saved; photo only-	Malaysia (Sandakan, Sabah)	B.M.M	1999	+	
H. sp. A 4	(97)	- specimen not saved; photo only-	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. sp. A 5	(56)	- specimen not saved; photo only-	Malaysia (Sandakan, Sabah)	B.M.M	1999		+
H. sp. A 6	(13)	CSIRO H5284.05	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. sp. A 7	(99)	CSIRO H5478.01	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	+
H. sp. A 8	(123)	UMS MMKK136	Malaysia (Kota Kinabalu, Sabah)	B.M.M	1999	+	
H. sp. A 9	MMPL11	- specimen not saved-	India (Cochin)	P. Last	1999	+	+
H. sp. E 1	NG1a	CSIRO H5155.01	Indonesia (Irian Jaya)	P. Kailola	1999	+	+
H. sp. E 2	NG2a	CSIRO H4915.01	Indonesia (Irian Jaya)	P. Kailola	1999	+	+
H. sp. F	K5	CSIRO H5472.01	Malaysia (Kuching, Sarawak)	B.M.M	1999	+	+

continued...

Appendix **4.1.1.** continued

Species	Sample code	Specimen Registration Number	Locality	Collector	Year collected	16S	cyt. *b*
amphi-American *Himantura*							
H. pacifica	HP	ROM ICH66838	Guyana (Atlantic Ocean beach)[b]	N. Lovejoy	1992	+	+
H. schmardae	HS1b	ROM ICH66845	Costa Rica (Playa Panama)[d]	N. Lovejoy	1992	+	+

[a] 75% ethanol; [b] 95% ethanol, liver tissue; [c] frozen; [d] buffered DNA extract.
^ Siliman University Marine Laboratory - World Wildlife Fund for Nature Philippines.

Appendix 4.1.2. Optimal PCR conditions (Mg concentration and annealing temperature) in a 50 μl reaction volume used for obtaining 16S and cytochrome *b* sequences. Volumes of other reagents used are as described in the text (Section 4.1.2.2).

Species	sample code	16S		cyt b	
		[Mg] (mM)	annealing temperature (°C)	[Mg] (mM)	annealing temperature (°C)
<u>Indo-Pacific *Himantura*</u>					
H. chaophraya 1	SR99	2	55	2	55
H. chaophraya 2	SR105	2	55	2	55
H. chaophraya 3	DWPL1a	2	55	2	55
H. chaophraya 4	HC1	2	55	2	55
H. chaophraya 5	J3	2.5	55	x	x
H. chaophraya 6	J5	2	55	2	50
H. fai 1	(60)	2	55	x	x
H. fai 2	HF82	x	x	2	55
H. gerrardi 1	(50)	2	55	2	50
H. gerrardi 2	(52)	2	55	x	x
H. gerrardi 3	(5)	2	50, 55	x	x
H. gerrardi 4	(11)	2	55	x	x
H. gerrardi 5	(49)	2	50, 55	2	50
H. gerrardi 6	(7)	2, 2.5	50, 55	x	x
?H. gerrardi 7	(23)	2	55	x	x
?H. gerrardi 8	(108)	2	55	x	x
?H. gerrardi 9	MMPL7	2	55	x	x
?H. gerrardi 10	MMPL8	2	50	x	x
H. granulata 1	(124)	2	55	2	55
H. granulata 2	(125)	2	55	2	55
H. granulata 3	J1	2.5	55	2, 2.5	50
H. imbricata	MMPL2	2	50,55	2	50
H. jenkinsii 1	(22)	2.5	55	x	x
H. jenkinsii 2	BRU109	2.5	55	x	x
H. jenkinsii 3	JPAG213	2.5	55	x	x
H. oxyrhyncha	NUS10	2	55	2	55
H. pastinacoides	(62)	2	55	2	55
H. signifer 1	NUS1	2	55	x	x
H. signifer 2	NUS4	2	55	2	50, 55
H. signifer 3	NUS3	2	55	2	55
H. toshi 1	GY1	2	50	2	50
H. toshi 2	GY2	2	50	2	50
H. toshi 3	M7	x	x	2	50
H. uarnacoides 1	(20)	2	55	2	55
H. uarnacoides 2	(126)	2	55	x	x

continued...

Appendix 4.1.2. continued

Species	sample code	16S [Mg] (mM)	16S annealing temperature (°C)	cyt b [Mg] (mM)	cyt b annealing temperatu (°C)
Indo-Pacific *Himantura*					
H. uarnak 1	(2)	2	55	2	55
H. uarnak 2	(72)	2	55	2	55
H. uarnak 3	(89)	2.5	50, 55	2	55
H. uarnak 4	BRU111	2.5	55	x	x
H. uarnak 5	(29)	2	55	x	x
H. uarnak 6	EM330	2	55	2	55
H. uarnak 7	MMPK3	2	55	x	x
H. uarnak 8	MMPK7	2	55	2	55
H. uarnak 9	NTM1b	2	55	x	x
H. undulata 1	(27)	2.5, 2	50	x	x
H. undulata 2	(74)	2	50	2	55
H. undulata 3	(86)	2	55	2	50
H. walga 1	(15)	2	55	2	50
H. walga 2	(17)	2	55	x	x
H. sp. A 1	(3)	2	55	2	55
H. sp. A 2	(59)	2	55	2	55
H. sp. A 3	(84)	2	55	x	x
H. sp. A 4	(97)	2	55	2	55
H. sp. A 5	(56)	x	x	2	55
H. sp. A 6	(13)	2	55	2	55
H. sp. A 7	(99)	2	55	2	55
H. sp. A 8	(123)	2	55	x	x
H. sp. A 9	MMPL11	2	50, 55	2	55
H. sp. E 1	NG1a	2	55	2	55
H. sp. E 2	NG2a	2	55	2	55
H. sp. F	K5	2	55	2	55
amphi-American *Himantura*					
H. pacifica	HP	2	55	2	50
H. schmardae	HS1b	2	55	2	50

Appendix 4.2.1a. Aligned partial mitochondrial 16S nucleotide sequence data set (606 bp) indicating two ambiguous-alignment regions (bp 230-278 and bp 427-436) (in gray). Question marks (?) indicate missing data, dots (.) indicate matching base to the reference taxon, *H. chaophraya*, and dashes (-) within the sequence indicate gaps.

	10	20	30	40	50	60	70	80	90	100	110	120	130	140
1 *H. chaophraya* 1	TAAGAGGTCC	CGCCTGCCCT	GTGATATTTT	T-AACGGCCG	CGGTATCTTG	ACCGTGCGAA	GGTAGCGTAA	TCACTTGTCT	TTTAATTGAA	GGCCTGTATG	AAAGGCATAA	CGAGAGTTTA	TCTGTCTTTA	TTTTCCAATC
2 *H. chaophraya* 2	....	....	....	.-........	....	....	....	....	....	....	....	....	....	....
3 *H. chaophraya* 3	....	....	....	.-........	....	....	....	....	....	...T......	....	....	....	....
4 *H. chaophraya* 4	....	....	....	.T........	....	....	....	....	....	...T......	....	....	....	....
5 *H. chaophraya* 5	....	....	....	.-........	....	....	....	....	....	....	....	....	....	....
6 *H. chaophraya* 6	....	....	....	.-........	....	....	....	....	....	....	....	....	....	....
7 *H. fai* 1	....	....	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
8 *H. gerrardi* 1	???.......	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
9 *H. gerrardi* 2	??........	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
10 *H. gerrardi* 3	?.........	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
11 *H. gerrardi* 4	....	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
12 *H. gerrardi* 5	??........	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
13 *H. gerrardi* 6	??........	..T.......	....	.-........	....	....	....	...AC.....	....	....	..T.....T.	....	....	....
14 *?H. gerrardi* 7	??........	.A........	....	.T........	....	....	....	...AC.....	....	.......G..	..T.....T.	....	....	....
15 *?H. gerrardi* 8	??........	....	....	.T........	....	....	....	...AC.....	....	....	........T.	....	....	....
16 *?H. gerrardi* 9	....	....	....	.-........	....	....	....	...AC.....	....	....	..T.....T.	....	....	....
17 *?H. gerrardi* 10	??????????	??????????	??????....	.-........	T.........	....	....	...AC.....	....	....	..T.....T.	....	....	....
18 *H. granulata* 1	??.......T	G.........	.....TC...	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
19 *H. granulata* 2	.........T	....	....	.T........	....	....	....	....	....	....C.....	........T.	....	....	....
20 *H. granulata* 3	.........T	G.........	....	.T........	....	....	....	....	....	....C.....	........T.	....	....	....
21 *H. imbricata*	....	....	....	.-........	....	....	....	........T.	......A...	....C.....	........T.	....	A.........	....
22 *H. jenkinsii* 1	....	....	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
23 *H. jenkinsii* 2	??????.C.T	?.......A.	A..C.T....	.-........	T..A......	....	.......A..	....	....	....C.....	........T.	....	....	....
24 *H. jenkinsii* 3	???????G..	T.........	...C.T....	.-........	T..A......	....	....	....	....	....C.....	........T.	....	....	....
25 *H. oxyrhyncha*	??????????	???.......	....	.-........	...C......	....	....	........T.	......A...	....C.....	..T.....T.	....	A.........	..C.......
26 *H. pastinacoides*	....	....	....	.-........	....	....	.......C..	....	....	....	........T.	....	A.........	....
27 *H. signifer* 1	??????????	???.......	....	.-........	...C......	....	....	........T.	......A...	....C.....	..T.....T.	....	A.........	..C.......
28 *H. signifer* 2	....	....	....	.-........	....	....	....	........T.	......A...	....C.....	..T.....T.	....	A.........	..C.......
29 *H. signifer* 3	....	....	....	.-........	....	....	....	........T.	......A...	....C.....	..T.....T.	....	A.........	..C.......
30 *H. toshi* 1	....	....	....	.-........	....	....	....	...A......	.......A..	....C.....	........T.	....	....	....
31 *H. toshi* 2	??????????	??????????	??????????	?-????????	????......	....	.......A..	...A......	.......A..	....C.....	........T.	....	....	....
32 *H. uarnacoides* 1	?........T	....	....	.T........	....	....	.......C..	....	....	....C.....	........T.	....	....	..C.......
33 *H. uarnacoides* 2	.........T	....	....	.T........	....	....	.......C..	....	....	....C.....	........T.	....	....	..C.......
38 *H. uarnak* 5	.........T	....	....	.T........	....	....	....	....	....	....C.....	........T.	....	....	....
39 *H. uarnak* 6	???....G.T	T.........	....	.-........	.......C..	....	....	...T......	....	....C.....	........T.	....	....	....
40 *H. uarnak* 7	??????????	??????????	??????????	?-........	.......C..	....	....	...T......	....	....C.....	........T.	....	....	....
41 *H. uarnak* 8	.........T	....	....	.-........	.......C..	....	....	...T......	....	....C.....	........T.	....	....	....
42 *H. uarnak* 9	??.......T	....	....	.-........	.......C..	....	....	...T......	....	....C.....	........T.	....	....	....
43 *H. undulata* 1	.........T	....	....	.-........	.......T..	....	....	...T......	....	....C.....	........T.	....	....	....
44 *H. undulata* 2	???......T	....	....	.-........	.......T..	......A...	....	...T......	....	....C.....	........T.	....	....	....
45 *H. undulata* 3	.........T	....	....	.-........	.......T..	....	....	...T......	....	....C.....	........T.	....	....	....
46 *H. walga* 1	....	....	....	.-........	....	....	....	...A....T.	......A...	..A..C....	........T.	....	A.........	....
47 *H. walga* 2	....	....	....	.-........	....	....	....	...A....T.	......A...	..A..C....	........T.	....	A.........	....
48 *H.* sp. A 1	....	....	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
49 *H.* sp. A 2	??????????	?.....T...	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
50 *H.* sp. A 3	??????????	??????????	??????????	?-????????	??????????	??????????	????????..	....	....	....C.....	........T.	....	....	....
51 *H.* sp. A 4	....	....	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
52 *H.* sp. A 6	....	....	.....T....	.-........	....	....	....	...T......	....	....C.....	........T.	....	....	....
53 *H.* sp. A 7	????....G.	..T.......	.....T....	.-........	....	....	....	...T......	....	....C.....	........T.	....	....	....
54 *H.* sp. A 8	??........	....	.....T....	.-........	....	....	....	...T......	....	....C.....	........T.	....	....	....
55 *H.* sp. A 9	??........	......T...	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
56 *H.* sp. E 1	??????????	??????????	??????????	?-????????	??????????	??????????	???????...	....	....	....C.....	........T.	....	....	....
57 *H.* sp. E 2	....	....	....	.-........	....	....	....	....	....	....C.....	........T.	....	....	....
58 *H.* sp. F	.........T	....	....	.T........	....	....	....	....	....	....C.....	........T.	....	....	....
59 *H. pacifica*	....	....	.....T.A..	.-........	....	....	....	....	....	.A..C.....	..T.....T.	....	.......C..	....
60 *H. schmardae*	....	....	.....T.A..	.-........	....	....	....	.....C....	....	...TC.....	..C.......	....	C......C..	....

Appendix 4.2.1a. continued

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                              150        160        170        180        190        200        210        220        230        240        250        260        270        280        290        300
 1 H. chaophraya 1        AATGAAATTA GCCTTCTCGT GCAGAGACGA GAATATAAAC ATAAGACGAG AAGACCCTAT GGAGCTTTAA ACACCTAAGC TATCTCTAA- ----TGTA-- -AAC---TTA ----ATATCC TT-GGA--TA CAAC---ATT TAA-AAGAAA -TTTTAGCTT
 2 H. chaophraya 2        .......... .......... .......... .......... .......... .......... .......... .......... .........T G---TAAACT TAA---TATC ---------C TT-GGA--TA CAACA---.. ...--..G.. A.........
 3 H. chaophraya 3        .......... ....C..... ......G... .......... .......... .......... .......C.. .......... ..C......T ----GTAA-- --ACC-TA-C T----GTCC- TT-GGA--CA TAA---C.-C .C.A..-G.. ACC.....C.
 4 H. chaophraya 4        .......... ....C..... ......G... .......... .......... .......... .......C.. .......... ..C......- ---TGTAA-- -ACC---TAC ---T--GTCC TT-GGA--CA TAAC---.C. C.--..AG.. ACC.....C.
 5 H. chaophraya 5        .......... .......... .......... .......... .......... .......... .......... .......... .........- ----TGTA-- -AAC---TTA ----ATATCC TT-GGA--TA CAAC---... ...-..-G.. A.........
 6 H. chaophraya 6        .......... .......... .......... .......... .......... .......... .......... .......... .........T G-----TA-- -AAC---TT- ---AATATCC TT-GGA--TA CAAC---... ..--...G.. A.........
 7 H. fai 1               .......... AT..C..... .....AG... .G........ .......... .......... ....-..C.. ....T....T ...T.....A ----TAGA-- -AA---TATC T----GGCCC TT-GGG--CA TAACA---.C ...C-.AG.. A.A...A...
 8 H. gerrardi 1          .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT.....- ---ACATA-- -AAC---ACC ---CC-ACCT TC-GGG--TA CAAC---.C. A..C..-G.. G-CC.GA...
 9 H. gerrardi 2          .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT.....- ---ACATA-- -AAT---ACC C--C--ACCT TC-GGG--TA CAAC---.C. A..C..-G.. GCC.G.-...
10 H. gerrardi 3          .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT.....A ----CATA-- -AA---TACC C----CACCT TC-GGG--TA CAAC---.C. A..C-.AG.. CC-C.GA...
11 H. gerrardi 4          .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT....-- --AACATA-- -AAT---ACC ----C-CACC TT-CGG-GTA CAAC---.C. A..C..-G.. C-CC.GA...
12 H. gerrardi 5          .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT.....- ---ACATA-- -AAT---ACC C--C--ACCT TC-GGG--TA CAAC---.C. A..C..-G.. GCC.G.-...
13 H. gerrardi 6          .......... AT..C..... .....AG... .G........ .......... .......... .......C.. ....T....T ..CT.....A ----TATA-- -AA---TATC T----CACCT TC-GGG--TA CAACA---C. A..C-.AG.. G-CC.GA...
14 ?H. gerrardi 7         .......... AT..C..... .....AG... .G........ .......... .......... .......... ....T....T ..CT.....- ----TATA-- -AAT---ATC ----TCACCT TC-GGG--TA CAAC---.C. A..C..-G.. GCC.G.-...
15 ?H. gerrardi 8         .......... AT..C.C... .....AG..G .G........ .......... .......... .......C.. ....T....T ..CT.....- ---ACATA-- -AAT---ACC ---CC-ACCT TC-GGG--TA CAAC---.C. A..C..-G.. CCC.G.-...
16 ?H. gerrardi 9         .......... AT..C..... .....AG..G .G........ .......... .......... .......... ....T....T ..CT.....A ----TACA-- -AAT---ACC ----TCACCT TC-GGG--TA CAAC---.C. A..C...... --CC.GA...
17 ?H. gerrardi 10        .......... AT..C..... .....AG..G .G........ .......... .......... .......... ....T....T ..CT.....- ---ATATA-- -AAT---ACC ----TCACCT TC-GGG--TA CAA-C--.C. A..C...... --CC.GA...
18 H. granulata 1         .......... A...C.C... .T.......G .G...A.... .......... .......... .......C.. .T..T..... ..CT.....T -----ATA-- -AAT---TCC ACCCTA--CC TCTGGG--TA TAAT---.C. ...T...G.C -.CC......
19 H. granulata 2         .......... A...C.C... .T........ .G...A.... .......... .......... .......C.. .T..T..... ..CT....-- --AT-ATA-- -AATCCACC ----C-TACC TC-TGG-GTA TAAT---.C. ...T..-GG. C.CC......
20 H. granulata 3         .......... A...C.C... .T........ .G...A.... .......... .......... .......C.. .T..T..... ..CT.....T -----ATA-- -AAT---TCC ACCCTA--CC TCTGGG--TA TAAT---.C. ...T...G.C -.CC......
21 H. imbricata           .......... AT..C..... .....AG... .G........ .......... .......... .......... ....T....T .....-...A ----AACG-- -AA---TATA -----CATCC TC-GGA--TA TAAATA-CC. ...A-.AGT- --CT..A...
22 H. jenkinsii 1         .......... AT..C..... .....AG... .G..GC.... .......... .......... .......C.. ....T....T ..CT....TC TAGATACA-- -AAT---ATC A--CA-ACCC TC-GGG--TA TAAA---TA. CT.C..-G.. ACC...A...
23 H. jenkinsii 2         .......... AT..C..... .....AG... .G..GC.... .......... .......... .......C.. ....T....T ..CT....TC TAGATACA-- -AAT---ATC A--CA-ACCC TC-GGG--TA TAAA---TA. CT.C..-G.. ACC...A...
24 H. jenkinsii 3         .......... AT..C..... .....AG... .G..GC.... .......... .......... .......C.. ....T....T ..CT....TC TAGATACA-- -AAT---ATC A--CA-ACCC TC-GGG--TA TAAA---TA. CT.C..-G.. ACC...A...
25 H. oxyrhyncha          .......... AT..C..... .....AG... .GG..CT... .......... ........G. .......C.. ....T....T .....T...- ---AAATC-- -AAT---AC- ----TAATCC TC-GGA--TG TAAAT--... ...--.--.. GCCC..A...
26 H. pastinacoides       .......... AT..C..... .....AG... .G...C.... .......... .......... .......C.. ....T....T ...T.....- ---GTATA-- -AAC---ACA C--CTCACCT TC-GGG--TA TAAC---.C. C..C..-G.. G.C.G.-...
27 H. signifer 1          .......... AT..C..... .....AG... .GG..CT... .......... ........G. .......C.. ....T....T .....T..-- --AAAATC-- -AAT---ACT ----A-ATCC TC-GGATGTA -AAT---... ...A..-G-- C-CC..A...
28 H. signifer 2          .......... AT..C..... .....AG... .GG..CT... .......... ........G. .......C.. ....T....T .....T...A A----ATC-- -AAT---A-- ---CTAATCC TC-GGA--TG TAAA---TA. .T.A..AG-- -CCC..A...
29 H. signifer 3          .......... AT..C..... .....AG... .GG..CT... .......... ........G. .......C.. ....T....T .....T...A A----ATC-- -AAT---A-- ---CTAATCC TC-GGA--TG TAAA---TA. .T.A..AGC- --CC..A...
30 H. toshi 1             .......... AT..C..... .....AG... .G..G..... .......... .......... .......... ....T....T ...T.....A ----TATAC- -AAAA-CATC T----CGCCT TT-GGG--TA TAAA--T.C. ...T..-G.. G.C.-.A...
31 H. toshi 2             .......... AT..C..... .....AG... .G..G..... .......... .......... .......... ....T....T ...T.....- ---ATATACA AAAC---ATC ----TCGCCT TT-GGG--TA TAAAT--.C. ...T-.AG.. G-.C..A...
32 H. uarnacoides 1       .......... AT..CT.... .....AG... AG...C.... .......... .......... .......C.. ....T....T ..CT.....A ----CATA-- -AA---CACC A----CCCCC AC-GGG--CA TAATA---.. ...CC.AG.. CC.T..A...
33 H. uarnacoides 2       .......... AT..CT.... .....AG... AG...C.... .......... .......... .......C.. ....T....T ..CT.....- ---ACATA-- -AAC---ACC ----GCCCCC AC-GGG--CA TAA-T---.. ...CC.AG.. CC.T..A...
38 H. uarnak 5            .......... AT..C..... .....AG... .G...C.... .......... .......... .......C.. ....T....T ...T..C..A ----TATG-- -AAT---ATC ----TAATCC AC-GGA--TG TAAT---.C. C..C..-G.. G.C...A...
39 H. uarnak 6            .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....- ---ACATA-- -ATC---ATC ----TAGTCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
40 H. uarnak 7            .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....A C----ATA-- -ATC---AT- ---CTAATCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
41 H. uarnak 8            .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....A ----CATA-- -ATC---ATC ----TAGTCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
42 H. uarnak 9            .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....A C----ATA-- -ATC---AT- ---CTAATCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
43 H. undulata 1          .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....- ---ACATA-- -ACT---ATC ---CA-ATCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
44 H. undulata 2          .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....- ---ACATA-- -ACC---ATC ---CA-ATCC GC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
45 H. undulata 3          .......... AT..C..... .....AG... .G........ .......... .......... .......C.. .........T ...T.....- ---ACATA-- -ACT---ATC ----CAATCC AC-GGA--TA TAAC---.C. ...C..AG.. G.C...A...
46 H. walga 1             .......... AT..C..... .....AG... .G........ .......... .......... .......... ....T....T ..-TCT.G.A ----AATA-- -AA---TACG C----GTCCT T--GGA--TA TAAAT--.C. ...A-.AG-- TC-...A...
47 H. walga 2             .......... AT..C..... .....AG... .G........ .......... .......... .......... ....T....T .....-.G.- ---AAATA-- -AAT---A-C ----GCGTCC TT-GGA--TA TAAAT--.C. ...----... G.C...A...
48 H. sp. A 1             .......... AT..C..... .....AC... .G...C.... .......... .......... .......C.. .........T .........A ----CATA-- -ACC---ACC ----CAGTCT AC-GGA--TA TAAC---... ...C..-G.G G.C...A...
49 H. sp. A 2             .......... AT..C..... .....AC... .G...C.... .......... .......... .......C.. .........T .........A C----ATA-- -A------CC ACCCAG--TC TACGGA--TA TAAC---... ...C....GG -.C...A...
50 H. sp. A 3             .......... AT..C..... .....AC... .G...C.... .......... .......... .......C.. .........T .........A C----ATA-- -ACC---AC- ---CCAGTCT AC-GGA--TA TAAC---... ...-C.AG.G G.C...A...
51 H. sp. A 4             .......... AT..C..... .....AC... .G...C.... .......... .......... .......C.. .........T .........A ----CATA-- -ACC---ACC ----CAGTCT AC-GGA--TA TAAC---... ...C..-G.G G.C...A...
52 H. sp. A 6             .......... AT..C.C... .....AG... .G...C.... .......... .......... .......... .........T ...T.....- ---ACATA-- -ACC---TTC ---CA-ATCC AC-GGA--TA TAAC---... ...C..-G.. G.C...A...
53 H. sp. A 7             .......... AT..C.C... .....AG... .G...C.... .......... .......... .......... .......... ...T.....A ----CATA-- --ACC-TTCC A----ATCC- AC-GGA--TA TAA---C... ...C..-G.. G.C...A...
54 H. sp. A 8             .......... AT..C.C... .....AG... .G...C.... .......... .......... .......... .........T ...T.....A C----ATA-- -ACC---TT- ---CCAATCC AC-GGA--TA TAAC---... ...-C.AG.. G.C...A...
55 H. sp. A 9             .......... AT..C..... .....AG... .G...C.... .......... .......... .......C.. .........T .........A ----CATA-- -AC---CACC C----AGTCT AC-GGA--TA TAACA---.. ...C-.AG.G G.C...A...
56 H. sp. E 1             .......... AT..C..... .....AG... .G...C.... .......... .......... .......C.. ....T....T ...T.....G ----TAGA-- -AAT---ATC ----TCACCC TC-GGG--TA TAAC---..C ...C..-G.. G.C...A...
57 H. sp. E 2             .......... AT..C..... .....AG... .G...C.... .......... .......... .......C.. ....T....T ...T.....- ----GTAC-- --AAA-TATC T----CACCC TT-GGG--TA TAA---C..C ...C..-G.. G.C...A...
58 H. sp. F               .......... AT..C..... .....AG... ........C. .......... .......... .......C.. ....T..... ...T...-.A ----CACA-- -AACT-TAAA C-----TCCT C--GGA--TA TAACACC.CC A..C-.AG.. CCAC......
59 H. pacifica            .........G AT..C.C... .....AG... .....A.... .......... .......... .......... ....T....T ..C..T..T- --AACACC-- -CACA--ACC ----C-CTCT AC-GGA--CA CAAA---.CC A..ATT-..T CCAC..A...
60 H. schmardae           .........G AT..C..... .....AG... .....A.... .......... .......... .......... ....T....T ..C.CT...A C----ACA-- -CCC---AT- ---ACC-TCC AC-GGA--CT TAAA---CC. A..-.TT... CCCC..A...
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Appendix 4.2.1a. continued

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                                310        320        330        340        350        360        370        380        390        400        410        420        430        440        450        460
 1 H. chaophraya 1     AACTTGTTTT TGGTTGGGGC GACCAAGGAG AAAAACAAAG CCTCCTTATC GAATGTGTAA ACAATCACTA AAAAATTAGA ACTACTGTTC TAACTAATAG AAAA-TCTAA CGAACAATGA CCCAGGGAAC A---TTCC-- CTGATCAATG AACCAAGTTA
 2 H. chaophraya 2     .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ....-..... .......... ......GAAT A-TTC-..-- -......... ..........
 3 H. chaophraya 3     .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......G-AC T-AIT-..-- .......... ..........
 4 H. chaophraya 4     .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......G-AC T-AIT-..-- .......... ..........
 5 H. chaophraya 5     .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ....-..... .......... ......GAAC AIT---..-- .......... ..........
 6 H. chaophraya 6     .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ....-..... .......... ......G--A A-TAT...-- .......... ..........
 7 H. fai 1            .......... .........T .......... .........A .......... ........G. G.G......C .......... ......A... ...T...... ....-..... .......... ......GAGT A-CCC-..-- .......... ..........
 8 H. gerrardi 1       .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... ..........
 9 H. gerrardi 2       .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... ..........
10 H. gerrardi 3       .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAT --CCT-..-- .......... ..........
11 H. gerrardi 4       .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... ..........
12 H. gerrardi 5       .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... ..........
13 H. gerrardi 6       .......... .......... .......... ..G......A .......... ..G.....G. G..C.....C .......... ..C..CA... ...T...... ....A..... .......... ......GAGC C--CT-..-- .......... G.........
14 ?H. gerrardi 7      .......... .......... .......... ..G......A .......... ..G.....G. G..C.....C .......... ..C..CA... ...T...... ....A..... .......... ......GAGC C-C-T-..-- .......... G.........
15 ?H. gerrardi 8      .......... .......... .......... .........A .......... ..G.....G. CT.G.....C .......... G.C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... ..........
16 ?H. gerrardi 9      .......... .......... .......... ..G......A .......... ..G.....G. G..C.....C .......... ..C..CA... ...T...... ....A..... .......... ......GAGC C---CT.-- .......... G.........
17 ?H. gerrardi 10     .......... .......... .......... ..G......A .......... ..G.....G. G..C.....C .......... ..C..CA... ...T...... ....A..... .......... ......GAAC C--CT-..-- .......... G.........
18 H. granulata 1      .....A.... .......... .......... .........A .......... ........G. .T.......C .......... ......A... ...T...... ....A..... .......... ......G-AA T-ACT-..-- .......... ..........
19 H. granulata 2      .....A.... .......... .......... .........A .......... ........G. .T.......C .......... ......A... ...T...... ....A..... .......... ......GAAT A--CT-..-- .......... ..........
20 H. granulata 3      .....A.... .......... .......... .........A .......... ........G. .T.......C .......... ......A... ...T...... ....A..... .......... ......GAAT A--CT-..-- .......... ..........
21 H. imbricata        .......... .........T .......... .......T.A .......... ........G. TT.......C .......... .T....A... ...TC..... ....-..... .......... ......GAAC C-TCT-..-- .......... ..........
22 H. jenkinsii 1      .......... .........T .......... .....T...A .......... ...C....G. .T.......T .......... .T...CA... ...T...... ....-..... .......... ......GGAC A--CC-..-- .......... ..........
23 H. jenkinsii 2      .......... .........T .......... .....T...A .......... ...C....G. .T.......T .......... .T...CA... ...T...... ....-..... .......... ......GGAC A--CC-..-- .......... ..........
24 H. jenkinsii 3      .......... .........T .......... .....T...A .......... ...C....G. .T.......T .......... .T...CA... ...T...... ....-..... .......... ......GGAC A--CC-..-- .......... ..........
25 H. oxyrhyncha       ......C... .........T .......... .........A .......... ..GC...... TT...T...C ........A. ..C..CA..T ...T...... ..C.-..... ...C...... ......GAGC C-TCT-..-- .......... ..........
26 H. pastinacoides    ...C...... .......... .......... .......... .......... ...C....G. G........C T......... ..C...A... ...T...... ...G-..... .......... ......GGAC C--CT-..-- .......... G.........
27 H. signifer 1       ......C... .........T .......... .........A .......... ..GC...... TT...T...C ........A. ..C..CA..T ...T...... ..C.-..... ...C...... ......GAGC C-TCT-..-- .......... ..........
28 H. signifer 2       ......C... .........T .......... .........A .......... ..GC...... TT...T...C ........A. ..C..CA..T ...T...... ..C.-..... ...C...... ......GAGC C-TCT-..-- .......... ..........
29 H. signifer 3       ......C... .........T .......... .........A .......... ..GC...... TT...T...C ........A. ..C..CA..T ...T...... ..C.-..... ...C...... ......GAGC C-TCT-..-- .......... ..........
30 H. toshi 1          .......... .......... ....G..... .......... .......... ........G. G........C .......... ..C..CA... ...T...... ....-.T... .......... ......GAGC C-CT--..-- .......... ..........
31 H. toshi 2          .......... .......... ....G..... .......... .......... ........G. G........C .......... ..C..CA... ...T...... ....-.T... .......... ......GAGC C-C-T-..-- .......... ..........
32 H. uarnacoides 1    .......... .........T .......... .........A .......... ........G. G........C .......... ......A... ...T...... ...G-..... .......... ......GAAC A-CC--..-- .......... ..........
33 H. uarnacoides 2    .......... .........T .......... .........A .......... ........G. G........C .......... ......A... ...T...... ....-..... .......... ......GAAC A-C-C-..-- .......... ..........
38 H. uarnak 5         .......... .........T .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ..C.-..... .......... ......GACT ACTCT-..-- .......... G.........
39 H. uarnak 6         .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......GGAC C-TAT-..-- .......... ..........
40 H. uarnak 7         .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......G--GA C-TAT-..-- .......... ..........
41 H. uarnak 8         .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......GGAC T---AI.-- .......... ..........
42 H. uarnak 9         .......... .......... .......... .........A .......... ........G. .........C .......... .....CA... ...T...... ....-..... .......... ......G-GA C-TAT-..-- .......... ..........
43 H. undulata 1       .......... .......... .......... .........A .......... ........G. G........C .......... ......A... ...T...... ....-C.... .......... ......GATT A--TC-..-- .......... ..........
44 H. undulata 2       .......... .......... .......... .........A .......... ........G. G........C .......... ......A... ...T...... ....-C.... .......... ......GTTT A--TC-..-- .......... ..........
45 H. undulata 3       .......... .......... .......... .........A .......... ........G. G........C .......... ......A... ...T...... ...C-..... .......... ......GATT A-T-C-..-- .......... ..........
46 H. walga 1          .......... .........T .......... .......... .......... ........G. TT.......C .......... .T....A... ...TC..... ....-..... .......... ......GATC T-CCT-..-- .......... ..........
47 H. walga 2          .......... .........T .......... .......... .......... ........G. TT.......C .......... .T....A... ...TC..... ....-..... .......... ......GATC T-CCT-..-- .......... ..........
48 H. sp. A 1          .T........ .......... .......... .........A .......... ........G. G........C .......... ..C..CA... ...TC..... ....-..... .......... ......GGTT A-TCC-..-- .......... ..........
49 H. sp. A 2          .T........ .......... .......... .........A .......... ........G. G........C .......... ..C..CA... ...TC..... ....-..... .......... ......GGTT A-TCC-..-- .......... ..........
50 H. sp. A 3          .T........ .......... .......... .........A ...T...... ........G. G........C .......... ..C..CA... ...TC..... ....-..... .......... ......G-GT T-ATCC..-- .......... ..........
51 H. sp. A 4          .T........ .......... .......... .........A .......... ........G. G........C .......... ..C..CA... ...TC..... ....-..... .......... ......GGTT A-TCC-..-- .......... ..........
52 H. sp. A 6          .......... .......... .......... .........A .......... ........G. .........C .......... ......A... ...TC..... ....-..... ...G...... ......GGAC C-ACT-..-- .......... ..........
53 H. sp. A 7          .......... .......... .......... .........A .......... ........G. .........C .......... ......A... ...TC..... ....-..... ...G...... ......GGAC C-ACC-..-- .......... ..........
54 H. sp. A 8          .......... .......... .......... .........A .......... ........G. .........C .......... ......A... ...TC..... ....-..... ...G...... ......G-GA C-CACC..-- .......... ..........
55 H. sp. A 9          .T........ .........T .......... .........A .......... ........G. G........C .......... ..C..CA... ...TC..... ....-..... .......... ......GGTT A-TC--..-- .......... ..........
56 H. sp. E 1          .......... .........T .......... .........A .......... ........G. G.......CC .....C.... ..C...A... ...T...... ....-..... .......... ......GAAC --ACT-..-- .......... ..........
57 H. sp. E 2          .......... .........T .......... .........A .......... ........G. G.......CC .....C.... ..C...A... ...T...... ....-..... .......... ......G-AA C-ACT-..-- .......... ..........
58 H. sp. F            .......... .......... .......... .........A .......... ........G. .T.T.....C .......... ..C.-A.... ...T...... ....-..... .......... ......TAAT --TTT-T.-- ........C. ..........
59 H. pacifica         ...C...... .......... ........G. .........A ..C....... ....C.A.G. .-..C....T ....-..... GTC..CAC.. C..T...... ....-..... .......... .....AGATC C-CCT-T.TT .......... G.........
60 H. schmardae        ...C...... .......... ........G. .........A ..C....... ....C...GT C--.C....- -....C.... .T...CA... ...T...... ..C.-..... .......... T....----A A-ACTCTT-- .......... G.........
```

Appendix 4.2.1a. continued

```
                              470        480        490        500        510        520        530        540        550        560        570        580        590        600     606
 1 H. chaophraya 1      CCCTAGGGAT AACAGCGCAA TCCTTTTCAA GAGCCCTCAT CACCGAAAGG GTTTACGACC TCGATGTTGG ATCAAGACAT TCTAATGGTG TAGCAGCTAT TAA-GGGTTC GTTTGTTCAA CGATTAAAGT CCTACGTGAT CTGAGT
 2 H. chaophraya 2      .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
 3 H. chaophraya 3      .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
 4 H. chaophraya 4      .......... .......... ......C... .......... .......... .......... .......... .......... .......... .......... ...-...... .......... .......... .......... ......
 5 H. chaophraya 5      .......... .......... ......C... .......... .......... ......C... .......... .......... C......... .......... ...-...... .......... .......... .......... ......
 6 H. chaophraya 6      .......... .......... ......C... ..A....... .......... .......... .......... .......... C......... .......... ...-...... .......T.. .......... .......... ......
 7 H. fai 1             .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C...T..... .......... ...-...... .....G-..T ?????????? ?????????? ??????
 8 H. gerrardi 1        .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
 9 H. gerrardi 2        .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
10 H. gerrardi 3        .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
11 H. gerrardi 4        .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
12 H. gerrardi 5        .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
13 H. gerrardi 6        .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... C......... C..-...... .......... .......... .......... ......
14 ?H. gerrardi 7       .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... C......... C..-...... .......... .......... .......... ......
15 ?H. gerrardi 8       .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... C..-...... .......... .......... .......... ......
16 ?H. gerrardi 9       .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... C......... C..-...... .....G.... .......... .......... ......
17 ?H. gerrardi 10      .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... C......... C..-...... .....G.... .......... .......... ......
18 H. granulata 1       .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C......... .......... ...-...... .........T .......... ......A... ......
19 H. granulata 2       .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
20 H. granulata 3       .......... .......... .......... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
21 H. imbricata         .......... .......... ......C... ......C... T......... .......... .......... ....G..... C......... C......... ...-...... .......... .......... T......... ......
22 H. jenkinsii 1       .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
23 H. jenkinsii 2       .......... .......... ......C... .......T.. ...A...... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
24 H. jenkinsii 3       .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
25 H. oxyrhyncha        ...C...... .......... ......C... ......C... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
26 H. pastinacoides     .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
27 H. signifer 1        ...C...... .......... ......C... ......C... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
28 H. signifer 2        ...C...... .......... ......C... ......C... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
29 H. signifer 3        ...C...... .......... ......C... ......C... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
30 H. toshi 1           .......... .......... ......C.C. .......... .......... .......... .......... .......... C......... ..-....... ...A...... ...-....G. .......... .....C.... ......
31 H. toshi 2           .......... .......... ......C.C. .......... .......... .......... .......... .......... C......... ..-....... ...A...... ...-....G. .......... .....C.... ......
32 H. uarnacoides 1     .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
33 H. uarnacoides 2     .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
38 H. uarnak 5          .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
39 H. uarnak 6          .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
40 H. uarnak 7          .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .....G.... .......... .......... ......
41 H. uarnak 8          .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
42 H. uarnak 9          .......... .......... .......... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
43 H. undulata 1        .......... .......... .......... .......T.. .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
44 H. undulata 2        .......... .......... ......C... .......T.. .......... .......... .......... ....G..... C......... ......A... C..-...... ...C?????? ?????????? ?????????? ??????
45 H. undulata 3        .......... .......... ......C... .......T.. .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
46 H. walga 1           .......... .......... ......C... ......C... T......... .......... .......... ....G..... C......... C......... ...-...... .......... .......... .......... ......
47 H. walga 2           .......... .......... ......C... ......C... T......... .......... .......... ....G..... C......... C......... ...-...... .......... .......... .......... ......
48 H. sp. A 1           .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
49 H. sp. A 2           .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
50 H. sp. A 3           .......... .......... ......C.C. .......... .......... .......... .......... ....C..... C......... .......... ...-...... .......... .......... .......... ......
51 H. sp. A 4           .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
52 H.' sp. A 6          .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .....A.... ...-...... .......... .......... .......... ......
53 H. sp. A 7           .......... .......... .......... .......... .......... .......... .......... .......... C......... .......... ...-...... .......... .......... .......... ......
54 H. sp. A 8           .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
55 H. sp. A 9           .......... .......... ......C.C. .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
56 H. sp. E 1           .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C...T..... .......... ...-...... .....G.... .......... .......... ......
57 H. sp. E 2           .......... .......... ......C... .......... ...A...... .......... .......... ....G..... C...T..... .......... ...-...... .......... .......... .......... ......
58 H. sp. F             .......... .......... ......C... .......... .......... .......... .......... ....G..... C......... .......... ...-...... .......... .......... .......... ......
59 H. pacifica          .......... .......... ......C.T. ......C... .G........ .......... .......... ....G..... C.......-. C......... ...-A..... .......... .......... .......... ......
60 H. schmardae         .......... .......... ......C... .......A.. ...A...... .......... .......... ....G..... C......... C..A...... ...-...... .......... .......... ..C....... ......
```

Appendix 4.2.1b. Aligned amino acid sequences of the partial cytochrome *b* gene data set (318 bp) corresponding to positions 109-426 of the full length of cytochrome *b* gene of the stingray *H. signifer* (Sezaki *et al*. 1999). Question marks (?) indicate missing data, dots (.) indicate matching base to the reference taxon, H. signifer, and dashes (-) within the sequence indicate gaps.

	1																																					38
	Leu	Leu	Gly	Leu	Cys	Leu	Ile	Ile	Gln	Ile	Leu	Thr	Gly	Leu	Phe	Leu	Ala	Met	His	Tyr	Thr	Ala	Asp	Ile	Ser	Ser	Ala	Phe	Ser	Ser	Val	Ala	His	Ile	Cys	Arg	Asp	Val
1 *H. signifer* 3	TTA	CTG	GGC	CTA	TGC	CTA	ATT	ATC	CAA	ATC	CTT	ACA	GGT	TTA	TTC	CTA	GCT	ATA	CAT	TAT	ACC	GCA	GAC	ATC	TCC	TCA	GCA	TTC	TCC	TCA	GTC	GCA	CAC	ATC	TGT	CGA	GAC	GTA
2 *H. signifer* 2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
3 *H. chaophraya* 1	???	???	???	...	...	...	...	...	...	...	..C	...	..A	C..	...	T..	..C	...	...	...	...	...	..T	...	...	...	...	...	..T	...	...	A..	..T	...	..C	...	...	..G
4 *H. chaophraya* 2	???	???	???	???	...	A..	...	...	...	...	..C	...	..A	C..	...	T..	..C	...	...	...	...	...	..T	...	...	...	...	...	..T	...	...	...	..T	...	..C	...	..T	..G
5 *H. chaophraya* 3	???	???	??T	...	...	...	...	..T	...	...	A..	...	..A	...	...	T..	...	...	...	...	...	...	..T	...	...	...	...	...	..T	...	...	...	..T	...	..C	...	..T	...
6 *H. chaophraya* 4	???	???	??T	...	...	...	...	..T	...	...	A..	...	..A	...	...	T..	...	...	...	...	...	...	..T	...	...	...	...	...	..T	...	...	...	..T	...	..C	...	..T	...
7 *H. chaophraya* 6	???	???	???	???	???	???	???	???	???	??A	..G	...	..A	...	...	...	..C	...	...	...	..T	...	..T	...	...	...	...	...	..T	...	..T	...	..T	...	..C	...	...	...
8 *H. fai* 2	???	??.	..T	..C	...	...	...	...	...	...	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	..T	...	...	..T	...	..T	...	...	...	...	...
9 *H. gerrardi* 1	...	T..	...	..C	..T	.T.	..C	...	...	...	...	...	..G	..G	...	..G	..C	...	...	...	..T	...	...	G..	...	...	...	...	..T	..C	...	...	...	...	..C	...	..T	...
10 *H. gerrardi* 5	...	T..	...	..C	..T	.T.	..C	...	...	...	...	...	..G	..G	...	..G	..C	...	...	...	..T	...	...	G..	...	...	...	...	..T	..C	...	...	...	...	..C	...	..T	...
11 *H. granulata* 1	...	T..	...	..C	...	...	...	...	...	...	..C	...	..A	...	..T	...	...	...	..C	..C	...	...	..T	...	...	...	...	...	..T	...	..T	...	..T	..T	...	...	..T	...
12 *H. granulata* 2	...	T..	...	..C	...	...	...	...	...	...	..C	...	..A	...	..T	...	...	...	..C	..C	...	...	..T	...	...	...	...	...	..T	...	..T	...	..T	..T	...	...	..T	...
13 *H. granulata* 3	...	T..	...	..C	...	...	...	...	...	...	..C	...	..A	...	..T	...	...	...	..C	..C	...	...	..T	...	...	...	...	...	..T	...	..T	...	..T	..T	...	...	..T	...
14 *H. imbricata*	??.	..A	..T	...	...	...	...	...	...	...	...	...	..G	...	...	T..	..A	...	...	...	..T	...	..T	...	..A	...	...	...	..T	...	...	...	...	...	...	...	...	...
15 *H. oxyrhyncha*	??.	..A	..T	..C	...	...	...	...	...	...	...	...	..G	C..	...	...	...	...	..C	..C	...	...	...	...	...	...	...	...	...	...	...	..T	...	...	...	...	...	...
16 *H. pastinacoides*	...	...	..T	..C	...	..T	...	C.T	...	...	...	...	..G	..G	...	..G	..C	...	...	..C	..T	...	..T	G..	...	...	...	...	...	..C	..T	.TT	...	...	..C	...	...	...
17 *H. toshi* 1	...	T..	..T	..C	..T	..T	...	...	...	...	...	...	..G	...	...	...	..C	...	...	...	...	...	...	G..	...	...	...	...	...	..C	...	...	...	...	..C	...	..T	...
18 *H. toshi* 2	...	T..	..T	..C	..T	..T	...	...	...	...	...	...	..G	...	...	...	..C	...	...	...	...	...	...	G..	...	...	...	...	...	..C	...	...	...	...	..C	...	..T	...
19 *H. toshi* 3	??.	T..	..T	..C	..T	..T	...	...	...	...	...	...	..A	...	...	...	..C	...	...	...	...	...	...	G..	...	...	...	...	...	..C	...	...	...	...	..C	...	..T	...
20 *H. uarnacoides* 1	C..	...	..T	..C	..T	T..	...	...	...	...	...	...	..G	...	...	T..	...	...	...	...	..T	...	...	...	...	..C	...	...	...	...	..T	...	..T	..T	..C	...	...	...
21 *H. uarnak* 1	...	...	...	..T	...	T.G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	..G	...	...	...	...	...	..T	..T	...	...	...	..T	...
22 *H. uarnak* 2	...	T..	...	..T	...	T.G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	..G	...	...	...	...	...	..T	..T	...	...	...	..T	...
23 *H. uarnak* 3	...	T..	...	..T	...	T.G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	..G	...	...	...	...	...	..T	..T	...	...	...	..T	...
24 *H. uarnak* 6	...	...	..T	..T	...	..G	...	G..	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	..T	...	...	...	...	..T	...
25 *H. uarnak* 8	...	...	..T	..T	..T	..G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	.T.	...	...	...	...	...	..T	..T	...	...	...	...	..T	...
26 *H. undulata* 2	???	???	...	..T	..T	T.G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	..C	..T	...	...	...	..T	...
27 *H. undulata* 3	???	???	...	..T	..T	..G	...	...	...	...	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	..C	..T	...	...	...	..T	...
28 *H. walga* 1	??.	..A	..T	...	..T	...	...	...	...	...	...	...	..G	...	...	T..	..A	...	...	..C	..T	...	..T	...	..A	...	...	...	..T	...	...	...	..T	...	...	...	...	...
29 *H.* sp. A 1	...	...	..T	..C	...	T..	..C	...	...	G..	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T	...	...	...	..T	...
30 *H.* sp. A 2	...	...	..T	..C	...	T..	..C	...	...	G..	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T	...	...	...	..T	...
31 *H.* sp. A 4	...	...	..T	..C	...	T..	..C	...	...	G..	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T	...	...	...	..T	...
32 *H.* sp. A 5	...	...	..T	..C	...	T..	..C	...	...	G..	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T	...	...	...	..T	...
33 *H.* sp. A 6	...	...	..T	..C	...	...	..C	...	...	...	...	...	..G	...	...	T..	...	..G	...	...	...	...	..T	...	...	...	...	...	...	...	..T	...	..T	...	...	...	..T	...
34 *H.* sp. A 7	...	...	..T	..C	...	T.G	...	...	...	...	...	...	..G	...	...	...	...	..G	...	...	...	...	..T	...	...	...	...	...	...	...	..T	...	..T	...	...	...	...	...
35 *H.* sp. A 9	...	T..	..T	..C	...	T..	..C	...	...	G..	...	...	..G	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T	...	..C	...	..T	...
36 *H.* sp. E 1	...	...	..T	..C	...	...	..C	..T	...	...	...	...	..G	..G	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	A..	...	...	...	...	...	...	...
37 *H.* sp. E 2	...	...	..T	..C	...	...	..C	..T	...	...	...	...	..G	..G	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	A..	...	...	...	...	...	...	...
38 *H.* sp. F	?..	..A	.CT	..C	...	...	..C	G..	...	..T	..C	...	..A	C..	...	...	..A	...	...	..C	...	...	..T	...	..A	...	...	...	..T	...	A..	...	..T	..T	...	...	...	..T
39 *H. pacifica*	?.G	..A	...	..C	..T	...	...	...	...	...	..C	..C	..G	...	...	...	...	...	...	..C	...	...	..T	G..	..A	...	..C	...	...	...	A..	...	...	...	..C	...	...	...
40 *H. schmardae*	???	..A	...	T..	...	...	...	...	...	...	..C	..G	..G	C..	...	...	..A	...	..C	..C	...	C..	..T	...	..A	...	..C	...	...	...	A..	...	..T	...	.CC	...	...	...

Appendix 4.2.1b. continued

```
                         39                                                                                                                                                                                  77
                         Asn Tyr Gly Trp Leu Ile Arg Asn Thr His Ala Asn Gly Ala Ser Leu Phe Phe Ile Cys Ala Tyr Leu His Ile Ala Arg Gly Phe Tyr Tyr Gly Ser Tyr Leu Tyr Lys Glu Ala

 1 H. signifer 3         AAC TAC GGC TGA CTG ATC CGC AAC ACC CAT GCT AAT GGT GCC TCC CTA TTT TTT ATC TGT GCC TAT CTC CAT ATC GCT CGA GGC TTT TAC TAT GGC TCC TAC CTT TAT AAA GAG GCC
 2 H. signifer 2         ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..C ... ... ... ... ... ... ... ...
 3 H. chaophraya 1       ... ..T ... ... T.A ... ... ..T .T. ... ..C ..C ... ... ... A.. ... ..C ... ..C ATT ... ..T ... ..T ... ... ..T C.. ... ... ..T ..T ..T ... ..C ... ..A A..
 4 H. chaophraya 2       ... ..T ... ... T.A ... ... ..T .T. ... ..C ..C ... ... ... A.. ... ..C ... ..C ATT ... ..T ... ..T ... ... ..T C.C ... ... ..T ..T ..T ... ... ... ..A A..
 5 H. chaophraya 3       ... ..T ... ... T.A ... ... ..T .T. ... ..C ..C ... ... ... A.. ..C ..C ... ... .TT ... ..T ... ..T ... ... ... C.. ..T ... ..T ..T ..T ... ... ... ..A A.A
 6 H. chaophraya 4       ... ..T ... ... T.A ... ... ..T .T. ... ..C ..C ... ... ... A.. ..C ..C ... ... .TT ... ..T ... ..T ... ... ... C.. ..T ... ..T ..T ..T ... ... ... ..A A.A
 7 H. chaophraya 6       ... ..T ... ... T.A ..T ..A ..T .TT ... ... ..C ..C ... ..T ... ... ..C ... ... AT. ... ..T ... ..T ..C ... ..T C.C ... ... ... ..T ..T A.. ... ... ..A A..
 8 H. fai 2              ... ..T ... ... T.A ... ... ... .T. ... A.. ... ... ... ..T A.G ..C ... ... ..C .T. ... T.. ... ... ... ... ..T ... ..T ... ... ..T ..T ... ... ... ..A A..
 9 H. gerrardi 1         ... ..T ... ... T.A ... ..T ... CT. ... ..C ..C ..C ...     ... ... ..C ..T ... .TT ..C ..A ... ..T ..C ... ..T ..C ... ... ... ... ..T ... ... ... ..A A..
10 H. gerrardi 5         ... ..T ... ... T.A ... ..T ... CT. ... ..C ..C ..C ...     ... ... ..C ..T ... .TT ..C ..A ... ..T ..C ... ..T ..C ... ... ... ... ..T ... ... ... ..A A..
11 H. granulata 1        ... ..T ..T ... ..A ... ... ... .T. ... ..C ..C ... ... ..T A.. ... ... ..T ..C .T. ..C ... ... ... ..C ... ... C.C ... ... ... ... ..T ... ... ... ..A A..
12 H. granulata 2        ... ..T ..T ... ..A ... ... ... .T. ... ..C ..C ... ... ..T A.. ... ... ..T ..C .T. ..C ... ... ... ..C ... ..T C.C ... ... ... ... ..T ... ... ... ..A A..
13 H. granulata 3        ... ..T ..T ... ..A ... ... ... .T. ... ..C ..C ... ... ..T A.. ... ... ..T ..C .T. ..C ... ... ... ..C ... ..T C.C ... ... ... ... ..T ... ... ... ..A A..
14 H. imbricata          ... ..T ... ... ..A ... ... ..T ..T ... ..C ... ... ... ..T A.. ... ... ... ..C .T. ..C ... ... ... ... ... ..T ..C ... ..C ... ... ... ... ... ... ... A..
15 H. oxyrhyncha         ... ..T ... ... T.A ... ... ... .TT ..C ... ... ... ... ..A ... ... ... ... ..C ... ... A.. ... ... ... ... ..T ..C ... ..C ... ..A ... ... ... ... ... A..
16 H. pastinacoides      ... ..T ... ... T.A ... ... ..T .T. ..C ..C ..C ... ..T ... A.G ..C ... ... ... .TT ..C ... ... ..T ..C ... ... ... ... ..C ..T ... ..T ... ... ... ..A A..
17 H. toshi 1            ..T ..T ... ... T.A ... ..T ... .TT ... ..C ..C ... ..T ... A.. ..C ... ... ... .TT ..C ... ..C ..T ..C ... ... ..C ..T ... ... ... ..T ... ..C ... ... A..
18 H. toshi 2            ..T ..T ... ... T.A ... ..T ... .TT ... ..C ..C ... ..T ... A.. ..C ... ... ... .TT ..C ... ..C ..T ..C ... ... ..C ..T ... ... ... ..T ... ..C ... ... A..
19 H. toshi 3            ..T ..T ... ... T.A ... ..T ... .TT ... ..C ..C ... ..T ... A.. ..C ... ... ... .TT ..C ... ..C ..T ..C ... ... ..C ..T ... ... ..A ..T ... ..C ... ... A..
20 H. uarnacoides 1      ... ..T ... ... T.A ... ... ... .TT ... ... ..C ..C ... ... A.. ..C ..C ... ... .T. ... ..T ... ... ..C ... ..T ..C ... ... ... ... ... ... ... ... ..A A..
21 H. uarnak 1           ... ..T ... ... ..A ... ... ... .T. ..C ..C ... ... ... ... A.G ..C ... ... ..C ATT ... ..T ..C ..T ... ... ..T ... ... ... ... ... ..T ... ... ... ..A A..
22 H. uarnak 2           ... ..T ... ... ..A ... ... ... .T. ..C ..C ... ... ... ... A.G ..C ... ... ..C ATT ... ..T ..C ..T ... ... ..T ... ... ... ... ... ..T ... ... ... ..A A..
23 H. uarnak 3           ... ..T ... ... ..A ... ... ... .T. ..C ..C ... ... ... ... A.G ..C ... ... ..C ATT ... ..T ..C ..T ... ... ..T ... ... ... ... ... ..T ... ... ... ..A A..
24 H. uarnak 6           ... ..T ... ... ..A ... ... ... .T. ... ..C ..C ... ... ... A.G ..C ... ... ..C ATT ... ..T ..C ..T ... ... ..T ... ..T ..C ... ... ..T ..A ... ... ... A..
25 H. uarnak 8           ... ..T ... ... ..A ... ... ... .T. ... ..C ..C ... ... ... A.G ..C ... ... ..C ATT ... ..T ..C ..T ... ... ..T ... ..T ..C ... ... ..T ..A ... ... ... A..
26 H. undulata 2         ... ... ... ... ..A ... ... ... .T. ... ..C ..C ..C ... ..T A.G ..C ... G.. ..C .T. ... ..T ..C ..T ... ..G ..T ... ... ... ..T ..T ..T ..C ... ... ... A..
27 H. undulata 3         ... ... ... ... ..A ... ... ... .T. ... ..C ..C ..C ... ..T A.G ..C ... G.. ..C .T. ..C ..T ..C ..T ... ..G ..T ... ... ... ..T ... ..T ..C ... ... ... A..
28 H. walga 1            ..T ..T ... ... ..A ... ... ... ..T ... ..C ..C ..C ..T ..T A.. ..C ... ... ..C .TT ... ... ... ... ... ... ..T ..C ... ... ... ... ... ... ... ... ... A..
29 H. sp. A 1            ... ..T ... ... ..A ... ... ... .T. ..C ... ..C ..C ... ... A.G ..C ... ... ..C ATT ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ... ... ... ... A..
30 H. sp. A 2            ... ..T ... ... ..A ... ... ... .T. ..C ... ..C ..C ... ... A.G ..C ... ... ..C ATT ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ... ... ... ... A..
31 H. sp. A 4            ... ..T ... ... ..A ... ... ... .T. ..C ... ..C ..C ... ... A.G ..C ... ... ..C ATT ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ... ... ... ... A..
32 H. sp. A 5            ... ..T ... ... ..A ... ... ... .T. ..C ... ..C ..C ... ... A.G ..C ... ... ..C ATT ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ... ... ... ... A..
33 H. sp. A 6            ... ..T ... ... ..A ... ... ... .T. ..C ..C ..C ..C ... ... A.G ..C ... ... ..C .T. ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ..C ... ... ... A..
34 H. sp. A 7            ... ..T ... ... T.A ..T ... ..T .T. ..C ..C ..C ..C ... ... A.. ..C ... ... ... .TT ... ..T ... ..T ..C ... ..T ... ... ... ..T ... ... ... ... ... ... A..
35 H. sp. A 9            ... ..T ... ... ..A ... ... ... .T. ..C ... ..C ..C ... ... A.G ..C ... ... ..C ATT ..C ..T ..C ..T ... ... ..T ... ... ... ..T ... ..T ... ... ... ... A..
36 H. sp. E 1            ... ..T ... ... T.A ... ... ... .T. ... ..C ... ... ... ..T A.. ..C ... ... ... .T. ... T.. ... ..T ..C ... ..T C.. ..T ..C ... ... ..T ..C ..C ... ..A A..
37 H. sp. E 2            ... ..T ... ... T.A ... ... ... .T. ... ..C ... ... ... ..T A.. ..C ... ... ... .T. ... T.. ... ..T ..C ... ..T C.. ..T ..C ... ... ..T ..C ..C ... ..A A..
38 H. sp. F              ... ... ... ... ..A ... ... ..T .TT ... ... ... ..C ... ..T A.. ... ... ... ..C CTT ..C ..T ... ... ..C ... ... C.. ..T ..C ..T ... ..T ... ..C ... ..A A..
39 H. pacifica           ... ..T ..T ... ..A ... ... ... .TT ..C ... ..C ... ... ... A.. ..C ... ... ... .T. ..C ... ..C ... ... ..C ..A C.A ... ..C ... ..T ... ..A A.C ... ..A A..
40 H. schmardae          ... ... ... ... ..A ... ... ... ... ..C ... ... ..G ... ... A.. ..C ... ... ... A.. ..C ..A ... ... ..C ... ..G C.A ... ..C ... ..T ... ..A A.C ... ..A A..
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Appendix 4.2.1b. continued

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                      78                                                                                                                 106
                      Trp Asn Ile Gly Val Ile Ile Leu Val Leu Leu Met Ala Thr Ala Phe Val Gly Tyr Val Leu Pro Trp Gly Gln Met Ser Phe Trp

 1 H. signifer 3      TGA AAT ATT GGC GTA ATC ATC TTA GTG TTA CTA ATA GCT ACC GCC TTT GTA GGT TAT GTC CTC CCT TGA GGA CAA ATA TCA TTC TGA
 2 H. signifer 2      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
 3 H. chaophraya 1    ... ... ... ..A ... ..T ... ... T.A ... T.. ... ..C ..T ... ..C ..G ... ... ..T ..T ... ... ... ... ... ... ... ...
 4 H. chaophraya 2    ... ... ... ..A ... ..T ... ... T.A ... T.. ... ..C ..T ... ... ..G ..C ... ..T ..T ... ... ... ... ... ... ... ...
 5 H. chaophraya 3    ... ... ... ..A ... ..T ..T ... T.A ... T.. ... ..C ..T ... ... ... ..C ... ..T ..T ... ... ... ... ... ... ... ...
 6 H. chaophraya 4    ... ... ... ..A ... ..T ..T ... T.A ... T.. ... ..C ..T ... ... ... ..C ... ..T ..T ... ... ... ... ... ... ... ...
 7 H. chaophraya 6    ... ... ... ..A ... ..T ... ... T.A ... ... ... ... ... ... ... ... ..C ... ..T ..T ..C ... ... ... ... ... ... ...
 8 H. fai 2           ... ..C ... ... ..T ... ... ... ... C.. ... ... ... ..T ... ... ... ... ... ... ... ..C ... ... ... ... ... ... ...
 9 H. gerrardi 1      ... ... ... ..A ... ..T ... C.. ..A C.. ... ... ..C ..T ... ... ... ..C ... ... ... ..A ... ... ... ... ... ... ...
10 H. gerrardi 5      ... ... ... ..A ... ..T ... C.. ..A C.. ... ... ..C ..T ... ... ... ..C ... ... ... ..A ... ... ... ... ... ... ...
11 H. granulata 1     ... ... ... ..A ... ..T ..T ... C.A ... ... ... ... ... ... ... ... ... ... ..T ... ..C ... ... ... ... ... ... ...
12 H. granulata 2     ... ... ... ..A ... ..T ..T ... C.A ... ... ... ... ... ... ... ... ... ... ..T ... ..C ... ... ... ... ... ... ...
13 H. granulata 3     ... ... ... ..A ... ..T ..T ... C.A ... ... ... ... ... ... ... ... ... ... ..T ... ..C ... ... ... ... ... ... ...
14 H. imbricata       ... ..C ... ..A ... G.. C.. ... ... ... ..T ... ... ... ... ... ... ... ... ..T ..T ..C ... ... ... ... ... ... ...
15 H. oxyrhyncha      ... ..C ..C ..A ... ... ... ... ... .C. ... ... ..C ... ... ... ..G ... ... ... ..T ... ... ... ... ... ... ... ...
16 H. pastinacoides   ... ... G.. ..G ..C ..T ... C.. ... ... ... ... ... ..T ... ..C ... ... ... ... ..T ..A ... ... ... ... ... ... ...
17 H. toshi 1         ... ..C ... ..A ... ... ... ... ... ... ... ... ... ..T ... ..C ... ..C ... ..G ..T ..A ... ... ... ... ... ... ...
18 H. toshi 2         ... ..C ... ..A ... ... ... ... ... ... ... ... ... ..T ... ..C ... ..C ... ..G ..T ..A ... ... ... ... ... ... ...
19 H. toshi 3         ... ..C ... ..A ... ... ... ... ... ... ... ... ... ..T ... ..C ... ..C ... ..G ..T ..A ... ... ... ... ... ... ...
20 H. uarnacoides 1   ... ..C ... ..A ... ..T ... ... ... ... ... ... ... ..T ... ..C ... ... ... ..T ..T ..A ... ... ... ... ... ... ...
21 H. uarnak 1        ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ... ... ... ..C ..T ..T ..A ... ... ... ... ... ... ...
22 H. uarnak 2        ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ... ... ... ..C ..T ..T ..A ... ... ... ... ... ... ...
23 H. uarnak 3        ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ... ... ... ..C ..T ..T ..A ... ... ... ... ... ... ...
24 H. uarnak 6        ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ... ... ... ... ..T ..T ..A ... ... ... ... ... ... ...
25 H. uarnak 8        ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ... ... ... ... ..T ..T ..A ... ... ... ... ... ... ...
26 H. undulata 2      ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ..C ... ..C ... ..T ... ..A ... ... ... ... ... ... ...
27 H. undulata 3      ... ... ..C ..A ... ..T ... C.. A.A C.. ... ... ..C ..T ... ..C ... ..C ..C ..T ..T ..A ... ... ... ... ... ... ..?
28 H. walga 1         ... ..C ... ..A ... G.. C.. ... ... ... ... ... ..C ... ... ... ... ... ... ... ..T ..C ... ... ... ... ... ... ...
29 H. sp. A 1         ... ..C ..C ..A ... ... ... ... A.. C.. ..G ... ... ..T ... ... ... ... ... ... ... ..A ... ... ... ... ... ... ...
30 H. sp. A 2         ... ..C ..C ..A ... ... ... ... A.. C.. ..G ... ... ..T ... ... ... ... ... ... ... ..A ... ... ... ... ... ... ...
31 H. sp. A 4         ... ..C ..C ..A ... ... ... ... A.. C.. ..G ... ... ..T ... ... ... ... ... ... ... ..A ... ... ... ... ... ... ...
32 H. sp. A 5         ... ..C ..C ..A ... ... ... ... A.. C.. ..G ... ... ..T ... ... ... ... ... ... ... ..A ... ... ... ... ... ... ...
33 H. sp. A 6         ... ... ..C ..A ... G.. ... ... A.A C.. ... ... ... ..T ... ... ... ... ..C ... ..T ..A ... ... ... ... ... ... ...
34 H. sp. A 7         ... ... ..C ..G ... ... ... ... A.A ... ... ... ..C ..T ... ..C ... ..C ... ... ..T ..A ... ... ... ... ... ... ...
35 H. sp. A 9         ... ..C ..C ..A ... ... ... ... A.. C.. ... ... ... ..T ... ... ... ... ..C ... ... ..A ... ... ... ... ... ... ...
36 H. sp. E 1         ... ... ... ..A ..G ..T ... C.. C.A ... ... ... ..C ..T ... ..C ... ... ... ... ..T ..C ... ... ... ... ... ... ...
37 H. sp. E 2         ... ... ... ..A ..G ..T ... C.. C.A ... ... ... ..C ..T ... ..C ... ... ... ... ..T ..C ... ... ... ... ... ... ...
38 H. sp. F           ... ... ... ..T ... ..T ... C.. T.A ..G T.. ... ..C ..T ... ..C ... ..C ... ... ..T ..A ... ... ... ... ... ... ...
39 H. pacifica        ... ... ... ..A ... ..T ..T C.C C.A ... ..T ... ATC ..T ... ... ... ..C ... ... ... ..C ... ... ... ... ... ... ...
40 H. schmardae       ... ..C ... ..A ... ... ..T C.. T.A C.. ..T ... .T. ..T ..A ..C ... ..C ..C ... ... ..C ... ... ... ... ... ... ...
```

Appendix 4.2.2a. HKY85 genetic distances (below diagonal), and number of substitutions (transition/transversion) for each pair-wise comparison (above diagonal) for partial 16S sequences.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1 H. varnak 1	—	0/2	4/1	0/1	7/3	2/3	1/1	1/2	2/2	9/5	12/5	8/7	9/5	9/3	12/4	8/4	11/4	6/2	7/3	4/2	17/5	18/8	18/8	17/8	16/8	18/7	18/8	16/7	20/8	20/8	15/5	16/8	15/5	15/5	14/5	10/3	12/4
2 H. varnak 2	0.004	—	4/1	0/1	7/3	2/3	1/2	1/2	2/2	9/5	12/5	8/6	9/5	9/2	12/3	8/3	11/4	6/2	7/4	4/2	17/5	16/8	18/8	17/8	16/8	18/7	18/8	16/7	20/8	20/8	15/5	16/8	15/5	15/5	14/5	10/4	12/4
3 H. varnak 3	0.009	0.009	—	4/0	9/2	6/2	5/2	5/1	4/1	13/4	16/4	12/6	13/4	13/2	14/3	12/3	15/3	8/1	10/3	8/1	19/4	18/5	20/5	19/5	18/5	20/6	20/7	18/8	22/7	22/7	17/4	18/5	17/4	17/4	16/4	12/4	14/3
4 H. varnak 4	0.002	0.002	0.007	—	7/2	2/2	1/2	1/1	2/1	9/4	12/4	8/6	9/4	9/2	12/3	8/3	11/3	6/1	7/3	4/1	17/4	16/5	18/5	17/5	16/5	18/6	18/7	16/6	20/7	20/7	15/4	16/5	15/4	15/4	14/4	10/4	12/3
5 H. varnak 5	0.019	0.019	0.021	0.017	—	9/2	8/2	8/1	9/1	12/4	14/4	12/6	12/4	14/2	17/3	13/3	12/3	13/1	14/3	11/1	18/4	17/5	19/5	18/5	17/5	17/6	17/7	17/6	18/7	18/7	17/4	18/5	12/4	14/4	13/4	10/4	11/3
6 H. varnak 6	0.009	0.009	0.015	0.007	0.021	—	0/1	1/1	2/1	11/4	13/3	9/5	11/4	11/2	14/3	10/3	13/3	6/1	7/3	4/1	17/4	16/5	18/5	17/5	16/5	18/6	18/7	16/6	20/7	19/6	15/4	15/4	17/4	17/4	16/4	11/3	14/3
7 H. varnak 7	0.004	0.006	0.014	0.006	0.020	0.002	—	0/1	1/1	9/4	12/4	9/6	9/4	9/1	11/1	8/2	10/3	5/1	6/2	3/1	15/4	14/5	16/5	15/5	14/5	15/6	15/7	14/6	18/5	19/5	13/4	15/5	15/4	16/4	15/4	11/2	12/3
8 H. varnak 8	0.006	0.006	0.011	0.004	0.017	0.004	0.002	—	1/0	10/3	13/3	9/5	10/3	10/1	13/2	9/2	12/2	5/0	6/2	3/0	16/3	15/4	17/4	16/4	15/4	17/5	17/6	15/5	19/6	19/6	14/3	15/4	16/3	16/3	15/3	11/3	13/2
9 H. varnak 9	0.007	0.007	0.009	0.006	0.019	0.006	0.004	0.002	—	11/3	14/3	10/5	11/3	11/1	12/2	10/2	13/2	4/0	7/2	4/0	17/3	16/4	16/4	17/4	16/4	18/5	18/6	16/5	20/6	20/6	15/3	16/4	17/3	17/3	16/3	12/3	14/2
10 H. sp. A 1	0.026	0.026	0.032	0.025	0.030	0.028	0.026	0.025	0.026	—	3/0	1/2	0/0	10/4	13/5	9/5	0.006	13/3	14/5	11/3	18/6	17/7	19/7	18/7	17/7	18/6	18/7	17/8	19/7	20/7	15/4	17/5	14/6	16/6	15/6	9/6	9/5
11 H. sp. A 2	0.033	0.033	0.039	0.031	0.035	0.031	0.032	0.031	0.033	0.006	—	4/2	3/0	13/4	16/4	13/5	0.010	16/3	17/5	14/3	21/6	20/7	23/6	21/6	20/7	22/6	21/7	20/7	20/7	20/7	18/4	20/5	17/6	19/5	18/5	11/6	12/5
12 H. sp. A 3	0.032	0.030	0.039	0.030	0.039	0.030	0.032	0.030	0.032	0.006	0.013	—	1/2	11/5	12/5	10/4	0.009	12/5	13/6	10/5	19/8	18/9	20/8	19/9	18/9	18/7	18/9	18/10	21/9	21/9	14/6	16/5	14/6	15/6	14/6	10/8	10/7
13 H. sp. A 4	0.026	0.026	0.032	0.025	0.030	0.028	0.026	0.025	0.026	0.000	0.006	0.006	—	10/4	13/5	9/5	0.006	13/3	14/5	11/3	18/6	17/7	19/7	18/7	17/7	18/6	18/7	17/8	19/7	20/7	15/4	17/5	14/6	16/6	15/6	9/6	9/5
14 H. sp. A 6	0.023	0.021	0.029	0.021	0.030	0.025	0.020	0.021	0.023	0.026	0.033	0.035	0.026	—	5/1	1/1	0.029	13/1	14/3	11/1	20/4	19/5	21/5	20/5	19/5	21/6	21/7	19/6	22/7	23/6	18/4	20/4	18/4	18/4	17/4	13/3	13/3
15 H. sp. A 7	0.030	0.029	0.032	0.029	0.038	0.033	0.024	0.029	0.027	0.034	0.039	0.037	0.034	0.011	—	4/2	0.037	14/2	17/4	14/2	23/5	22/6	24/8	23/6	22/6	22/7	24/8	22/7	25/8	25/6	19/5	20/4	21/5	21/5	20/5	15/3	16/4
16 H. sp. A 8	0.023	0.021	0.029	0.021	0.031	0.025	0.020	0.021	0.023	0.027	0.035	0.030	0.027	0.004	0.011	—	0.027	12/2	13/4	10/2	19/5	18/6	20/5	19/6	18/6	20/6	20/8	18/7	22/8	23/7	16/5	18/4	17/5	17/3	16/3	12/4	12/4
17 H. sp. A 9	0.029	0.029	0.034	0.027	0.029	0.031	0.026	0.027	0.029	2/1	4/1	2/2	2/1	12/3	15/4	11/3	—	15/2	16/4	13/2	20/5	19/6	21/6	20/6	19/6	20/5	20/6	19/7	22/8	22/6	17/3	18/4	16/5	16/4	15/4	8/5	9/4
18 H. undulata 1	0.015	0.015	0.017	0.013	0.027	0.013	0.012	0.009	0.007	0.030	0.037	0.037	0.030	0.027	0.031	0.027	0.033	—	3/2	1/0	20/3	19/4	21/4	20/4	19/4	20/5	20/6	19/5	22/6	22/6	17/3	18/4	17/3	17/3	16/3	12/3	14/2
19 H. undulata 2	0.020	0.022	0.026	0.020	0.035	0.020	0.017	0.016	0.018	0.038	0.046	0.044	0.038	0.035	0.043	0.035	0.041	0.010	—	2/2	19/5	18/6	20/6	19/6	18/6	19/7	19/8	18/7	21/7	21/7	16/4	17/5	18/5	18/5	17/5	13/3	15/4
20 H. undulata 3	0.011	0.011	0.017	0.009	0.023	0.009	0.008	0.006	0.007	0.026	0.033	0.032	0.026	0.023	0.031	0.023	0.029	0.002	0.008	—	18/4	17/5	19/5	18/5	17/5	18/6	18/7	17/6	20/7	20/7	15/3	16/4	15/3	15/3	14/3	10/3	12/2
21 H. gerrardi 1	0.042	0.042	0.044	0.040	0.042	0.040	0.039	0.037	0.039	0.046	0.054	0.061	0.046	0.047	0.055	0.047	0.049	0.045	0.049	0.043	—	2/1	0/1	0/1	2/1	9/4	12/5	2/2	8/5	9/5	21/4	21/5	18/6	23/6	22/6	19/6	19/5
22 H. gerrardi 2	0.042	0.042	0.044	0.040	0.042	0.040	0.039	0.036	0.038	0.046	0.053	0.061	0.046	0.046	0.055	0.046	0.048	0.044	0.049	0.042	0.006	—	2/2	2/2	0/0	11/5	10/4	0/1	10/6	11/6	20/4	21/6	18/5	21/7	20/7	18/7	18/6
23 H. gerrardi 3	0.046	0.046	0.048	0.044	0.046	0.044	0.043	0.040	0.042	0.050	0.058	0.063	0.050	0.050	0.059	0.048	0.052	0.048	0.053	0.046	0.002	0.007	—	0/0	2/2	9/5	12/6	2/1	9/5	10/5	22/5	20/6	20/7	22/4	21/4	20/7	20/6
24 H. gerrardi 4	0.044	0.044	0.046	0.042	0.044	0.042	0.041	0.038	0.040	0.048	0.053	0.063	0.048	0.048	0.057	0.048	0.050	0.046	0.051	0.044	0.002	0.007	0.000	—	2/2	9/5	12/6	2/1	8/5	9/5	21/5	21/6	19/7	23/5	22/5	19/7	19/6
25 H. gerrardi 5	0.042	0.042	0.044	0.040	0.042	0.040	0.039	0.036	0.038	0.046	0.053	0.061	0.046	0.046	0.055	0.046	0.048	0.044	0.049	0.042	0.006	0.000	0.007	0.007	—	11/5	10/4	0/1	10/6	11/6	20/4	21/6	18/5	21/7	20/7	18/7	18/6
26 H. gerrardi 6	0.048	0.048	0.050	0.046	0.044	0.046	0.043	0.042	0.044	0.046	0.056	0.056	0.046	0.053	0.057	0.051	0.049	0.049	0.054	0.047	0.025	0.030	0.027	0.027	0.030	—	5/1	11/6	4/1	4/1	19/4	18/5	17/8	23/7	22/7	18/8	19/7
27 H. gerrardi 7	0.050	0.050	0.052	0.048	0.046	0.048	0.045	0.044	0.046	0.048	0.055	0.061	0.048	0.055	0.063	0.055	0.051	0.050	0.056	0.048	0.033	0.027	0.034	0.034	0.027	0.011	—	10/5	6/2	6/2	19/4	19/6	17/7	22/9	21/9	18/9	19/8
28 H. gerrardi 8	0.044	0.044	0.046	0.042	0.044	0.042	0.041	0.038	0.040	0.048	0.053	0.063	0.048	0.048	0.056	0.048	0.050	0.046	0.051	0.044	0.007	0.002	0.006	0.006	0.002	0.032	0.029	—	10/6	11/6	20/5	21/7	18/6	21/6	20/6	18/8	18/7
29 H. gerrardi 9	0.050	0.054	0.056	0.052	0.048	0.052	0.047	0.048	0.050	0.050	0.053	0.068	0.050	0.056	0.065	0.058	0.054	0.054	0.058	0.052	0.025	0.030	0.027	0.025	0.030	0.009	0.015	0.030	—	1/0	20/5	21/6	18/9	25/8	24/8	20/7	20/8
30 H. gerrardi 10	0.053	0.057	0.059	0.055	0.051	0.050	0.049	0.050	0.052	0.055	0.055	0.068	0.055	0.059	0.064	0.061	0.057	0.057	0.061	0.055	0.028	0.034	0.030	0.028	0.034	0.010	0.016	0.034	0.002	—	21/5	21/6	19/9	25/8	24/8	20/7	21/8
31 H. toshi 1	0.038	0.038	0.040	0.036	0.040	0.037	0.035	0.032	0.035	0.036	0.043	0.044	0.036	0.042	0.047	0.041	0.039	0.038	0.041	0.035	0.049	0.047	0.053	0.050	0.047	0.045	0.045	0.049	0.049	0.053	—	2/1	17/5	23/6	22/6	16/6	16/5
32 H. toshi 2	0.046	0.044	0.048	0.044	0.049	0.040	0.042	0.040	0.042	0.047	0.053	0.047	0.047	0.051	0.051	0.047	0.047	0.046	0.050	0.042	0.056	0.058	0.056	0.058	0.058	0.049	0.053	0.060	0.058	0.057	0.008	—	18/7	20/6	19/6	18/6	18/6
33 H. pastinacoides	0.038	0.038	0.040	0.036	0.030	0.040	0.039	0.036	0.038	0.038	0.045	0.049	0.038	0.042	0.051	0.042	0.040	0.038	0.047	0.034	0.048	0.044	0.052	0.050	0.044	0.048	0.046	0.046	0.052	0.057	0.042	0.053	—	16/6	17/6	13/6	13/5
34 H. uarnacoides 1	0.038	0.038	0.040	0.036	0.034	0.040	0.041	0.036	0.038	0.042	0.047	0.046	0.042	0.042	0.050	0.038	0.038	0.038	0.047	0.034	0.056	0.054	0.050	0.054	0.054	0.059	0.060	0.052	0.065	0.068	0.057	0.055	0.042	—	1/0	12/4	13/3
35 H. uarnacoides 2	0.036	0.036	0.038	0.034	0.032	0.038	0.039	0.034	0.036	0.040	0.045	0.044	0.040	0.040	0.048	0.036	0.037	0.036	0.045	0.032	0.054	0.052	0.048	0.052	0.052	0.057	0.058	0.050	0.062	0.065	0.054	0.053	0.044	0.002	—	11/4	12/3
36 H. sp. E 1	0.028	0.030	0.035	0.030	0.030	0.030	0.028	0.030	0.032	0.033	0.037	0.039	0.033	0.035	0.039	0.035	0.028	0.032	0.037	0.028	0.056	0.056	0.061	0.058	0.056	0.058	0.061	0.058	0.061	0.060	0.049	0.055	0.042	0.035	0.032	—	0/1
37 H. sp. E 2	0.030	0.030	0.032	0.028	0.026	0.032	0.031	0.028	0.030	0.026	0.033	0.037	0.026	0.030	0.038	0.030	0.025	0.030	0.039	0.027	0.046	0.046	0.050	0.048	0.046	0.050	0.052	0.048	0.054	0.059	0.040	0.051	0.034	0.030	0.028	0.002	—
38 H. sp. F	0.042	0.042	0.044	0.040	0.040	0.040	0.041	0.036	0.038	0.050	0.056	0.060	0.050	0.050	0.055	0.049	0.053	0.042	0.052	0.038	0.045	0.044	0.040	0.042	0.044	0.055	0.057	0.042	0.059	0.062	0.056	0.057	0.050	0.046	0.044	0.048	0.042
39 H. chaophraya 1	0.061	0.061	0.059	0.059	0.063	0.059	0.058	0.055	0.053	0.057	0.060	0.071	0.057	0.055	0.051	0.057	0.063	0.057	0.072	0.057	0.078	0.076	0.080	0.078	0.076	0.083	0.080	0.076	0.079	0.086	0.063	0.074	0.065	0.072	0.069	0.075	0.063
40 H. chaophraya 2	0.053	0.053	0.059	0.051	0.057	0.051	0.050	0.047	0.049	0.051	0.058	0.063	0.051	0.049	0.053	0.047	0.055	0.053	0.063	0.049	0.072	0.070	0.072	0.072	0.070	0.074	0.074	0.070	0.078	0.084	0.061	0.069	0.059	0.061	0.059	0.068	0.057
41 H. chaophraya 3	0.044	0.044	0.050	0.042	0.048	0.042	0.041	0.038	0.040	0.046	0.051	0.058	0.046	0.050	0.055	0.049	0.049	0.048	0.058	0.044	0.057	0.052	0.057	0.056	0.052	0.063	0.061	0.052	0.065	0.070	0.061	0.071	0.058	0.057	0.054	0.060	0.050
42 H. chaophraya 4	0.046	0.042	0.048	0.044	0.046	0.044	0.041	0.040	0.042	0.050	0.058	0.060	0.050	0.053	0.053	0.053	0.053	0.050	0.060	0.046	0.057	0.052	0.057	0.056	0.052	0.063	0.061	0.052	0.067	0.072	0.059	0.067	0.057	0.061	0.058	0.068	0.059
43 H. chaophraya 5	0.056	0.057	0.063	0.055	0.061	0.055	0.054	0.050	0.053	0.054	0.060	0.066	0.054	0.052	0.053	0.052	0.059	0.057	0.067	0.053	0.076	0.073	0.076	0.075	0.073	0.078	0.078	0.073	0.080	0.086	0.061	0.069	0.063	0.067	0.065	0.072	0.061
44 H. chaophraya 6	0.059	0.059	0.065	0.057	0.063	0.057	0.056	0.053	0.055	0.057	0.064	0.069	0.057	0.055	0.055	0.055	0.061	0.059	0.067	0.055	0.078	0.076	0.078	0.078	0.076	0.080	0.080	0.076	0.084	0.090	0.063	0.071	0.065	0.069	0.067	0.075	0.063
45 H. walga 1	0.054	0.054	0.057	0.053	0.052	0.053	0.052	0.048	0.051	0.056	0.062	0.068	0.056	0.050	0.059	0.047	0.055	0.052	0.063	0.049	0.061	0.059	0.061	0.061	0.059	0.063	0.063	0.059	0.067	0.072	0.055	0.062	0.059	0.055	0.053	0.065	0.054
46 H. walga 2	0.048	0.049	0.051	0.047	0.047	0.047	0.045	0.043	0.045	0.048	0.052	0.060	0.048	0.044	0.053	0.043	0.047	0.046	0.056	0.043	0.060	0.059	0.063	0.061	0.059	0.061	0.063	0.061	0.061	0.066	0.049	0.060	0.053	0.059	0.057	0.058	0.049
47 H. imbricata	0.050	0.050	0.053	0.049	0.046	0.049	0.048	0.044	0.047	0.046	0.053	0.056	0.046	0.046	0.055	0.043	0.043	0.048	0.056	0.045	0.063	0.061	0.063	0.063	0.061	0.063	0.065	0.061	0.071	0.076	0.057	0.069	0.057	0.053	0.053	0.057	0.048
48 H. oxyrhyncha	0.066	0.066	0.068	0.064	0.060	0.066	0.072	0.066	0.068	0.064	0.068	0.075	0.064	0.073	0.077	0.070	0.062	0.075	0.087	0.071	0.073	0.075	0.075	0.075	0.075	0.077	0.081	0.077	0.082	0.088	0.082	0.085	0.073	0.068	0.066	0.072	0.064
49 H. signifer 1	0.068	0.068	0.070	0.066	0.062	0.068	0.074	0.068	0.070	0.064	0.066	0.074	0.064	0.075	0.079	0.073	0.062	0.077	0.089	0.073	0.077	0.079	0.075	0.075	0.079	0.081	0.086	0.077	0.086	0.090	0.084	0.089	0.075	0.070	0.068	0.074	0.066
50 H. signifer 2	0.070	0.071	0.073	0.069	0.064	0.075	0.075	0.070	0.073	0.066	0.074	0.081	0.066	0.077	0.086	0.075	0.063	0.079	0.091	0.075	0.075	0.077	0.075	0.075	0.077	0.080	0.088	0.077	0.087	0.094	0.084	0.092	0.075	0.073	0.073	0.081	0.068
51 H. signifer 3	0.070	0.071	0.073	0.069	0.064	0.075	0.075	0.070	0.073	0.066	0.074	0.081	0.066	0.077	0.086	0.075	0.063	0.079	0.091	0.075	0.077	0.079	0.077	0.077	0.079	0.081	0.088	0.079	0.089	0.096	0.083	0.094	0.075	0.075	0.075	0.081	0.068
52 H. granulata 1	0.056	0.052	0.058	0.054	0.054	0.054	0.051	0.052	0.054	0.062	0.065	0.069	0.062	0.054	0.059	0.054	0.069	0.058	0.064	0.056	0.058	0.060	0.062	0.058	0.060	0.079	0.081	0.060	0.077	0.076	0.071	0.073	0.069	0.063	0.061	0.060	0.058
53 H. granulata 2	0.042	0.042	0.044	0.040	0.042	0.042	0.043	0.038	0.040	0.052	0.051	0.062	0.052	0.046	0.051	0.044	0.057	0.044	0.054	0.042	0.050	0.052	0.050	0.048	0.052	0.065	0.069	0.050	0.067	0.070	0.059	0.064	0.056	0.050	0.048	0.058	0.050
54 H. granulata 3	0.046	0.046	0.044	0.044	0.044	0.044	0.045	0.042	0.040	0.052	0.055	0.062	0.052	0.048	0.048	0.048	0.059	0.044	0.058	0.046	0.052	0.054	0.056	0.052	0.054	0.069	0.071	0.054	0.071	0.072	0.061	0.066	0.058	0.056	0.054	0.058	0.052
55 H. fai 1	0.034	0.038	0.038	0.036	0.034	0.036	0.030	0.032	0.034	0.038	0.045	0.049	0.038	0.038	0.047	0.036	0.036	0.034	0.037	0.030	0.056	0.055	0.055	0.055	0.055	0.060	0.062	0.055	0.059	0.065	0.047	0.056	0.047	0.032	0.030	0.018	0.018
56 H. jenkinsii 1	0.040	0.040	0.042	0.038	0.032	0.042	0.041	0.038	0.040	0.046	0.051	0.059	0.046	0.046	0.054	0.046	0.042	0.048	0.058	0.044	0.050	0.048	0.050	0.050	0.048	0.059	0.061	0.046	0.062	0.068	0.054	0.064	0.048	0.038	0.038	0.046	0.038
57 H. jenkinsii 2	0.059	0.057	0.061	0.057	0.050	0.056	0.050	0.057	0.059	0.069	0.065	0.062	0.069	0.065	0.074	0.065	0.061	0.063	0.074	0.059	0.073	0.071	0.073	0.073	0.071	0.082	0.084	0.071	0.086	0.072	0.078	0.064	0.069	0.055	0.054	0.050	0.061
58 H. jenkinsii 3	0.052	0.052	0.054	0.050	0.044	0.046	0.045	0.050	0.052	0.059	0.055	0.060	0.059	0.057	0.065	0.057	0.051	0.061	0.072	0.057	0.063	0.061	0.063	0.063	0.061	0.071	0.073	0.061	0.075	0.068	0.067	0.064	0.061	0.050	0.050	0.046	0.051
59 H. pacifica	0.101	0.099	0.103	0.099	0.094	0.101	0.099	0.096	0.099	0.096	0.099	0.110	0.096	0.096	0.106	0.093	0.097	0.107	0.122	0.103	0.093	0.095	0.086	0.090	0.095	0.089	0.095	0.092	0.088	0.093	0.105	0.106	0.103	0.106	0.103	0.114	0.101
60 H. schmardae	0.100	0.099	0.103	0.099	0.088	0.101	0.098	0.096	0.099	0.101	0.105	0.121	0.101	0.099	0.108	0.101	0.104	0.103	0.115	0.098	0.100	0.101	0.099	0.097	0.101	0.095	0.099	0.099	0.094	0.100	0.107	0.116	0.099	0.101	0.101	0.109	0.096

continued...

Appendix 4.2.2a. continued.

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1 *H. uarnak* 1	15/7	27/4	23/4	18/5	20/4	24/5	26/4	19/9	18/7	17/9	26/7	25/9	25/11	24/12	20/9	18/4	19/5	12/5	15/6	19/11	18/9	35/15	31/19
2 *H. uarnak* 2	15/7	27/4	23/4	18/5	20/2	24/5	26/4	19/9	18/7	17/9	26/7	25/9	25/11	24/12	19/8	18/4	19/5	12/7	15/6	19/10	18/9	35/14	31/18
3 *H. uarnak* 3	17/6	27/3	27/3	22/4	22/3	28/4	30/3	21/8	20/6	19/8	28/6	27/8	27/10	26/11	22/8	20/3	19/4	13/6	17/5	21/10	20/8	37/14	33/18
4 *H. uarnak* 4	15/6	27/3	23/3	18/4	20/3	24/4	26/3	19/6	18/6	17/8	26/6	25/6	25/10	24/11	20/8	18/3	19/4	12/6	15/5	19/10	18/8	35/14	31/18
5 *H. uarnak* 5	15/6	29/3	26/3	21/4	21/3	27/4	29/3	19/8	18/6	16/8	24/8	23/8	23/10	22/11	20/8	19/3	19/4	11/6	12/5	16/10	15/8	33/14	29/15
6 *H. uarnak* 6	15/6	27/3	23/3	18/4	20/3	24/4	26/3	19/8	18/6	17/8	26/7	25/9	26/12	25/13	20/8	19/3	19/4	12/6	17/5	19/10	18/6	36/14	32/18
7 *H. uarnak* 7	14/6	25/3	21/3	16/4	18/2	22/4	24/3	17/8	16/6	15/8	26/8	25/10	24/12	23/13	19/6	18/3	19/3	10/4	15/5	17/7	16/6	34/12	30/16
8 *H. uarnak* 8	14/5	26/2	22/2	17/3	19/2	23/2	25/2	18/7	17/5	16/7	26/7	25/9	25/11	24/12	20/7	18/2	19/3	11/5	16/4	20/9	19/7	35/13	31/17
9 *H. uarnak* 9	15/5	25/2	23/2	18/3	20/2	24/3	26/2	19/7	18/5	17/7	27/7	26/9	26/11	25/12	21/7	19/2	18/3	12/5	17/4	21/9	20/7	36/12	32/17
10 *H. sp.* A 1	18/8	24/5	21/5	18/6	21/5	22/6	24/5	19/10	17/8	14/10	22/10	20/12	20/14	19/15	22/10	22/5	21/6	11/8	17/7	23/12	20/10	34/14	31/19
11 *H. sp.* A 2	21/7	25/5	24/5	20/6	24/5	24/6	27/5	22/9	18/8	17/10	24/10	22/11	23/14	22/15	24/9	22/4	23/5	14/8	19/7	21/12	19/9	35/13	32/19
12 *H. sp.* A 3	18/9	25/7	22/6	19/7	21/6	22/8	24/7	20/10	18/9	15/10	22/11	20/13	21/15	20/16	21/10	21/7	21/7	12/9	18/9	19/9	18/9	36/11	32/20
13 *H. sp.* A 4	18/8	24/5	21/5	18/6	21/5	22/6	24/5	19/10	17/8	14/10	22/10	20/12	20/14	19/15	22/10	22/5	21/6	11/8	17/7	23/12	20/10	34/14	31/19
14 *H. sp.* A 6	20/6	25/3	22/3	22/4	25/2	23/4	25/3	18/8	17/6	16/8	28/8	27/10	27/12	26/13	22/6	21/3	21/4	13/6	19/5	25/8	22/7	36/12	34/15
15 *H. sp.* A 7	21/7	22/4	23/4	23/5	24/3	22/5	24/4	21/9	20/7	19/9	30/8	29/10	30/13	29/14	23/7	22/4	20/5	16/7	22/6	28/9	25/8	39/13	37/16
16 *H. sp.* A 8	19/6	25/4	21/3	21/4	24/3	22/5	24/4	17/7	16/6	15/7	27/8	26/10	26/12	25/13	21/7	19/4	20/5	12/6	18/6	24/9	21/8	36/10	33/17
17 *H. sp.* A 9	20/7	28/4	24/4	20/5	23/4	25/5	27/4	19/9	17/7	14/8	22/9	20/11	20/12	19/13	26/9	25/4	25/5	11/7	17/5	21/10	18/8	36/12	33/18
18 *H. undulata* 1	17/5	27/2	25/2	22/3	24/2	26/3	28/2	20/7	19/5	18/7	30/7	29/9	29/11	28/12	23/7	21/2	20/3	12/5	21/4	23/9	24/7	40/13	34/17
19 *H. undulata* 2	18/7	30/4	28/4	23/5	25/4	27/5	28/4	21/9	20/7	18/9	31/9	30/11	30/13	29/14	24/7	22/4	23/5	13/5	22/6	24/11	25/9	41/15	34/19
20 *H. undulata* 3	15/5	27/2	23/2	20/3	22/2	24/3	26/2	18/7	17/5	16/7	28/7	27/9	27/11	26/12	21/8	19/3	20/4	10/5	19/4	21/9	22/7	38/13	32/17
21 *H. gerrardi* 1	17/6	34/5	31/5	23/6	24/5	32/6	34/5	25/6	26/4	24/8	28/8	28/10	26/12	26/13	20/10	21/5	21/6	19/8	19/7	25/12	22/10	32/14	34/15
22 *H. gerrardi* 2	16/7	32/6	29/6	20/7	21/6	30/7	32/6	23/7	25/5	22/9	28/9	28/11	26/13	26/14	20/11	21/6	21/7	18/9	17/8	23/13	20/11	32/15	34/16
23 *H. gerrardi* 3	17/4	35/5	30/6	22/7	23/6	31/7	33/6	26/5	27/5	24/8	28/9	28/9	26/12	26/13	22/10	22/4	23/6	19/8	18/8	24/13	21/11	32/11	34/15
24 *H. gerrardi* 4	17/5	34/5	30/6	22/7	23/6	31/7	33/6	26/5	26/5	24/8	28/9	28/9	26/12	26/13	20/10	21/4	21/6	18/9	18/6	24/13	21/11	32/13	34/14
25 *H. gerrardi* 5	16/7	32/6	29/6	20/7	21/6	30/7	32/6	23/7	25/5	22/9	28/9	28/11	26/13	26/14	20/11	21/8	21/7	18/9	17/8	23/13	20/11	32/15	34/16
26 *H. gerrardi* 6	22/6	34/7	30/7	24/8	25/7	31/8	33/7	22/10	23/8	21/11	28/10	28/12	27/13	27/14	28/12	26/7	27/8	19/10	22/8	28/13	25/11	33/11	30/17
27 ?*H. gerrardi* 7	22/7	32/8	29/8	22/9	23/8	30/9	32/8	21/11	23/9	20/13	29/11	29/13	28/15	28/16	28/13	27/8	27/9	19/11	21/10	27/15	24/13	34/13	31/18
28 ?*H. gerrardi* 8	16/6	32/6	28/7	19/8	20/7	29/8	31/7	24/6	25/6	22/9	28/10	28/10	26/13	26/14	20/11	21/5	21/7	17/10	16/9	22/14	19/12	32/14	34/15
29 ?*H. gerrardi* 9	24/6	32/8	31/8	24/9	26/8	31/9	34/8	24/10	22/9	23/13	29/11	30/12	29/15	29/16	26/13	27/7	27/9	20/9	22/10	28/15	25/13	32/12	29/18
30 ?*H. gerrardi* 10	24/8	33/8	32/8	25/9	27/8	32/9	35/8	25/10	23/9	24/13	30/11	31/12	30/15	30/16	26/11	27/7	27/8	21/9	23/10	23/12	22/11	33/11	30/17
31 *H. toshi* 1	21/8	27/5	26/5	25/6	25/5	25/6	27/5	20/8	19/6	19/10	30/10	29/12	28/14	27/15	26/10	25/5	25/6	16/7	21/7	27/12	24/10	38/14	34/19
32 *H. toshi* 2	18/9	28/6	26/6	26/7	26/5	25/7	27/6	20/9	21/7	21/11	28/11	28/13	27/15	27/16	25/9	24/6	25/6	17/8	22/8	23/7	22/8	36/12	33/19
33 *H. pastinacoides*	18/8	28/5	25/5	24/6	24/5	26/6	28/5	22/8	21/6	21/8	28/8	27/10	26/12	25/13	25/10	24/5	24/6	15/8	16/7	23/12	21/10	35/16	31/18
34 *H. uarnacoides* 1	19/5	32/4	27/4	23/6	26/5	28/6	30/5	21/7	23/7	20/7	25/9	25/10	25/12	25/13	25/7	23/3	24/5	11/5	16/4	19/9	19/7	40/12	35/15
35 *H. uarnacoides* 2	18/5	31/4	26/4	22/6	25/5	27/6	29/5	20/7	22/7	19/8	24/9	24/10	24/13	24/14	24/7	22/3	23/5	10/5	15/5	18/10	18/8	39/12	34/16
36 *H. sp.* E 1	14/8	28/5	25/5	21/6	26/4	26/6	28/5	19/10	18/8	16/10	22/10	21/12	22/14	21/15	21/6	21/5	21/5	6/2	16/5	17/6	16/5	35/14	32/15
37 *H. sp.* E 2	15/7	28/4	25/4	21/5	26/4	26/5	28/4	19/9	18/7	16/9	23/9	22/11	22/13	21/14	23/7	22/4	22/5	6/3	16/4	22/9	19/7	35/15	32/16
38 *H. sp.* F	—	27/6	22/7	16/8	19/7	23/8	25/7	21/9	21/10	19/11	26/12	26/12	25/15	25/16	18/11	16/5	17/7	14/8	18/9	22/14	21/12	30/11	30/18
39 *H. chaophraya* 1	0.065	—	5/0	18/2	18/2	3/1	6/0	32/7	27/7	30/8	39/9	39/9	40/12	39/13	27/9	26/3	24/5	25/7	32/6	38/11	35/9	44/13	42/15
40 *H. chaophraya* 2	0.057	0.009	—	14/2	17/2	1/1	3/0	27/8	26/7	25/7	37/9	35/10	35/11	34/12	24/9	22/4	23/5	20/7	28/5	34/10	31/8	42/13	40/15
41 *H. chaophraya* 3	0.046	0.038	0.031	—	4/2	15/3	17/2	26/8	27/7	23/8	33/9	32/10	32/9	32/10	20/10	19/5	19/6	17/8	22/4	28/9	25/7	35/14	31/16
42 *H. chaophraya* 4	0.050	0.038	0.037	0.011	—	16/3	18/2	28/8	29/7	25/8	36/9	35/10	33/12	33/13	22/8	21/4	22/5	22/7	21/6	27/10	24/9	38/13	32/16
43 *H. chaophraya* 5	0.061	0.007	0.004	0.034	0.036	—	2/1	28/9	27/8	26/9	36/10	36/11	36/13	35/14	24/10	23/5	23/6	21/8	29/7	35/12	32/10	43/15	41/16
44 *H. chaophraya* 6	0.063	0.011	0.006	0.036	0.038	0.006	—	30/8	29/7	28/8	40/9	38/10	38/10	37/13	27/9	25/4	26/5	23/7	31/6	37/11	34/9	45/14	43/16
45 *H. walga* 1	0.058	0.078	0.069	0.067	0.072	0.073	0.076	—	4/1	5/4	26/7	27/6	24/9	24/9	27/12	25/7	26/8	16/11	17/11	23/16	20/14	33/13	29/19
46 *H. walga* 2	0.061	0.067	0.065	0.067	0.071	0.069	0.071	0.009	—	4/5	25/6	25/7	24/9	23/10	26/12	25/7	25/8	16/10	20/9	26/14	23/12	31/15	29/18
47 *H. imbricata*	0.059	0.076	0.063	0.061	0.065	0.069	0.071	0.017	0.017	—	23/7	23/6	22/7	23/7	25/13	22/8	24/9	12/11	17/9	23/14	20/12	30/15	28/18
48 *H. oxyrhyncha*	0.077	0.099	0.095	0.086	0.093	0.099	0.102	0.067	0.062	0.060	—	0/1	1/3	1/4	33/13	32/9	32/9	25/12	24/11	27/16	24/13	39/16	40/17
49 *H. signifer* 1	0.077	0.100	0.093	0.086	0.093	0.097	0.100	0.067	0.064	0.058	0.002	—	1/3	1/3	32/13	30/9	31/9	23/14	23/13	26/16	24/15	40/15	41/16
50 *H. signifer* 2	0.079	0.105	0.093	0.082	0.090	0.099	0.101	0.065	0.065	0.057	0.008	0.008	—	0/0	33/17	30/12	32/13	23/15	22/9	28/14	25/12	38/19	40/19
51 *H. signifer* 3	0.081	0.105	0.093	0.084	0.092	0.099	0.101	0.065	0.065	0.059	0.010	0.008	0.000	—	32/18	29/13	31/14	22/16	22/10	28/15	25/13	38/19	40/19
52 *H. granulata* 1	0.056	0.071	0.065	0.058	0.059	0.067	0.071	0.078	0.075	0.075	0.094	0.092	0.100	0.100	—	3/6	3/4	22/7	23/9	27/11	25/11	41/13	38/17
53 *H. granulata* 2	0.040	0.057	0.051	0.046	0.048	0.054	0.057	0.063	0.063	0.059	0.084	0.079	0.083	0.083	0.017	—	2/2	20/7	22/6	26/11	25/9	39/11	37/14
54 *H. granulata* 3	0.046	0.056	0.055	0.048	0.052	0.056	0.061	0.067	0.065	0.065	0.083	0.082	0.090	0.090	0.013	0.007	—	21/8	22/7	26/11	24/10	40/11	37/17
55 *H. fai* 1	0.045	0.066	0.055	0.051	0.060	0.060	0.062	0.055	0.053	0.047	0.079	0.079	0.079	0.079	0.060	0.055	0.059	—	14/8	20/11	17/9	35/15	30/19
56 *H. jenkinsii* 1	0.052	0.075	0.065	0.050	0.052	0.071	0.073	0.054	0.057	0.050	0.070	0.072	0.060	0.062	0.062	0.054	0.056	0.040	—	6/5	3/3	31/17	29/16
57 *H. jenkinsii* 2	0.071	0.100	0.089	0.074	0.074	0.095	0.098	0.078	0.080	0.074	0.087	0.089	0.084	0.086	0.075	0.073	0.073	0.064	0.021	—	3/3	37/20	34/19
58 *H. jenkinsii* 3	0.065	0.089	0.079	0.063	0.065	0.084	0.087	0.067	0.070	0.063	0.077	0.079	0.073	0.075	0.071	0.067	0.067	0.054	0.011	0.011	—	34/19	32/18
59 *H. pacifica*	0.082	0.117	0.113	0.099	0.104	0.119	0.121	0.093	0.092	0.091	0.115	0.116	0.114	0.117	0.111	0.101	0.104	0.107	0.096	0.117	0.108	—	20/12
60 *H. schmardae*	0.097	0.117	0.113	0.095	0.097	0.116	0.121	0.097	0.094	0.093	0.120	0.121	0.119	0.121	0.112	0.103	0.110	0.105	0.090	0.109	0.102	0.063	—

Appendix 4.2.2b. HKY85 genetic distances (below diagonal), and number of substitutions (transition/transversion) for each pair-wise comparison (above diagonal) for partial cytochrome *b* sequences.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1 H. uarnak 1	—	1/0	1/0	12/1	13/1	23/1	23/1	23/1	23/1	23/1	28/1	23/1	21/0	20/0	35/6	35/6	39/4	39/4	40/5	40/4	38/2	34/3	34/3	45/8	33/4	30/4	31/6	31/6	35/8	39/7	39/9	37/6	33/6	34/6	39/3	38/3	38/3	32/4	40/14	40/18
2 H. uarnak 2	0.003	—	0/0	13/1	14/1	24/1	24/1	24/1	24/1	24/1	29/1	22/1	21/0	20/0	34/6	34/6	38/4	38/4	39/5	41/4	37/2	35/3	35/3	46/8	33/4	30/4	31/6	31/6	35/6	40/7	40/9	38/6	34/6	35/6	38/3	37/3	37/3	32/4	41/14	41/18
3 H. uarnak 3	0.003	0.000	—	13/1	14/1	24/1	24/1	24/1	24/1	24/1	29/1	22/1	21/0	20/0	34/6	34/6	38/4	38/4	39/5	41/4	37/2	35/3	35/3	46/8	33/4	30/4	31/6	31/6	35/8	40/7	40/9	38/6	34/6	35/6	38/3	37/3	37/3	32/4	41/14	41/18
4 H. uarnak 6	0.043	0.046	0.046	—	3/0	23/2	23/2	23/2	23/2	22/2	28/2	25/2	20/1	19/1	35/7	35/7	33/5	33/5	34/6	35/5	37/3	29/4	29/4	41/9	34/5	32/5	29/7	29/7	34/9	37/8	35/10	35/7	33/7	34/7	39/4	38/4	38/4	30/5	40/13	46/17
5 H. uarnak 8	0.046	0.050	0.050	0.010	—	24/2	24/2	24/2	24/2	23/2	29/2	26/2	19/1	18/1	34/7	34/7	32/5	32/5	33/6	37/5	38/3	30/4	30/4	44/9	35/5	33/5	30/7	30/7	35/9	36/8	36/10	36/7	34/7	35/7	40/4	39/4	39/4	31/5	39/13	47/17
6 H. sp. A 1	0.082	0.086	0.086	0.085	0.089	—	0/0	0/0	0/0	14/0	27/0	4/0	27/1	28/1	39/5	39/5	36/3	36/3	37/4	40/5	32/1	41/2	41/2	46/7	40/3	37/3	37/5	37/5	37/7	35/6	36/8	36/7	33/5	34/5	42/2	41/2	41/2	25/3	44/13	42/17
7 H. sp. A 2	0.082	0.086	0.086	0.085	0.089	0.000	—	0/0	0/0	14/0	27/0	4/0	27/1	28/1	39/5	39/5	36/3	36/3	37/4	40/5	32/1	41/2	41/2	46/7	40/3	37/3	37/5	37/5	37/7	35/6	36/8	36/7	33/5	34/5	42/2	41/2	41/2	25/3	44/13	42/17
8 H. sp. A 4	0.082	0.086	0.086	0.085	0.089	0.000	0.000	—	0/0	14/0	27/0	4/0	27/1	28/1	39/5	39/5	36/3	36/3	37/4	40/5	32/1	41/2	41/2	46/7	40/3	37/3	37/5	37/5	37/7	35/6	36/8	36/7	33/5	34/5	42/2	41/2	41/2	25/3	44/13	42/17
9 H. sp. A 5	0.082	0.086	0.086	0.085	0.089	0.000	0.000	0.000	—	14/0	27/0	4/0	27/1	28/1	39/5	39/5	36/3	36/3	37/4	40/5	32/1	41/2	41/2	46/7	40/3	37/3	37/5	37/5	37/7	35/6	36/8	36/7	33/5	34/5	42/2	41/2	41/2	25/3	44/13	42/17
10 H. sp. A 6	0.082	0.086	0.086	0.082	0.085	0.046	0.046	0.046	0.046	—	23/0	14/0	25/1	20/1	39/5	39/5	38/3	38/3	39/4	38/5	36/1	35/2	35/2	45/7	38/3	36/3	33/5	33/5	37/7	33/6	33/6	38/7	35/5	36/5	38/2	37/2	37/2	29/3	42/13	42/17
11 H. sp. A 7	0.082	0.086	0.086	0.082	0.085	0.046	0.046	0.046	0.046	0.046	—	29/0	28/1	29/1	37/5	37/5	34/3	34/3	35/4	30/5	29/1	34/2	34/2	39/7	33/3	32/3	28/5	28/5	27/7	34/6	38/6	35/7	33/5	34/5	43/2	42/2	42/2	35/3	42/13	42/17
12 H. sp. A 9	0.101	0.105	0.105	0.104	0.108	0.094	0.094	0.094	0.101	0.094	0.079	—	28/1	27/1	37/5	37/5	34/3	34/3	35/4	40/5	32/1	43/2	43/2	48/7	39/3	36/3	36/5	36/5	36/7	37/6	39/8	38/7	35/5	36/5	42/2	41/2	41/2	26/3	45/13	41/17
13 H. undulata 2	0.073	0.073	0.073	0.072	0.069	0.099	0.099	0.099	0.099	0.091	0.103	0.103	—	5/0	36/6	36/6	40/4	40/4	40/4	47/4	36/2	38/3	38/3	45/8	39/4	38/4	35/6	35/6	34/8	40/7	44/9	45/6	39/6	38/6	40/3	39/3	39/3	34/4	38/14	43/18
14 H. undulata 3	0.069	0.069	0.069	0.069	0.065	0.103	0.103	0.103	0.103	0.073	0.107	0.099	0.016	—	35/6	35/6	37/4	37/4	38/5	44/4	37/2	37/3	37/3	42/8	40/4	38/4	36/6	36/6	36/8	39/7	41/9	45/6	40/6	39/6	39/3	38/3	38/3	37/4	39/14	42/18
15 H. gerrardi 1	0.147	0.143	0.143	0.151	0.147	0.160	0.160	0.160	0.160	0.160	0.152	0.152	0.154	0.150	—	0/0	26/4	26/4	27/5	32/6	33/6	34/7	34/7	44/12	36/8	30/8	32/10	32/10	25/9	38/11	40/13	44/10	37/8	38/8	35/7	34/7	34/7	40/6	39/16	45/20
16 H. gerrardi 5	0.147	0.143	0.143	0.151	0.147	0.160	0.160	0.160	0.160	0.160	0.152	0.152	0.154	0.150	0.000	—	26/4	26/4	27/5	32/6	33/6	34/7	34/7	44/12	36/8	30/8	32/10	32/10	25/9	38/11	40/13	44/10	37/8	38/8	35/7	34/7	34/7	40/6	37/18	45/20
17 H. toshi 1	0.157	0.153	0.153	0.135	0.131	0.140	0.140	0.140	0.140	0.149	0.132	0.132	0.165	0.152	0.104	0.104	—	0/0	1/1	30/4	29/4	34/5	34/5	45/10	39/6	37/6	32/8	32/8	33/9	30/9	33/11	36/10	33/8	34/8	40/5	41/5	41/5	34/6	36/16	43/20
18 H. toshi 2	0.157	0.153	0.153	0.135	0.131	0.140	0.140	0.140	0.140	0.149	0.132	0.132	0.165	0.152	0.104	0.104	0.000	—	1/1	30/4	29/4	34/5	34/5	45/10	39/6	37/6	32/8	32/8	33/9	30/9	33/11	36/10	33/8	34/8	40/5	41/5	41/5	34/6	36/16	43/20
19 H. toshi 3	0.166	0.162	0.162	0.144	0.140	0.149	0.149	0.149	0.149	0.158	0.141	0.141	0.168	0.160	0.112	0.112	0.006	0.006	—	31/5	29/5	35/6	35/6	44/11	37/7	35/7	30/9	30/9	31/10	30/10	33/12	36/9	33/9	34/9	39/6	40/6	40/6	34/7	35/17	42/21
20 H. pastinacoides	0.161	0.165	0.165	0.143	0.152	0.165	0.165	0.165	0.165	0.156	0.123	0.165	0.187	0.163	0.135	0.135	0.119	0.119	0.128	—	36/6	31/7	31/7	41/12	39/8	41/8	34/10	34/10	36/10	40/11	38/13	42/10	38/10	39/10	43/7	44/7	44/7	39/6	39/18	44/22
21 H. uarnacoides 1	0.137	0.141	0.141	0.145	0.141	0.117	0.117	0.117	0.117	0.133	0.105	0.117	0.140	0.144	0.139	0.139	0.115	0.115	0.120	0.151	—	34/3	34/3	43/8	34/4	33/4	31/8	31/8	20/8	26/7	28/9	31/8	31/6	32/6	37/3	36/3	36/3	28/4	38/14	40/16
22 H. sp. E 1	0.132	0.136	0.136	0.115	0.120	0.158	0.158	0.158	0.158	0.133	0.128	0.167	0.152	0.148	0.147	0.147	0.139	0.139	0.148	0.134	0.132	—	0/0	35/7	37/1	41/1	32/3	32/3	38/5	39/6	35/8	35/7	34/5	35/5	41/0	40/0	40/0	28/3	35/11	40/15
23 H. sp. E 2	0.132	0.136	0.136	0.115	0.120	0.158	0.158	0.158	0.158	0.133	0.128	0.167	0.152	0.148	0.147	0.147	0.139	0.139	0.148	0.134	0.132	0.000	—	35/7	37/1	41/1	32/3	32/3	38/5	39/6	35/8	35/7	34/5	35/5	41/0	40/0	40/0	28/3	35/11	40/15
24 H. sp. F	0.200	0.205	0.205	0.186	0.200	0.201	0.201	0.201	0.201	0.196	0.169	0.210	0.204	0.190	0.211	0.211	0.208	0.208	0.208	0.197	0.191	0.152	0.152	—	29/7	31/7	33/9	33/9	30/11	40/9	38/11	40/14	45/10	44/10	38/7	39/7	39/7	46/8	37/16	33/18
25 H. chaophraya 1	0.136	0.136	0.136	0.144	0.149	0.163	0.163	0.163	0.163	0.154	0.133	0.158	0.163	0.168	0.164	0.164	0.170	0.170	0.165	0.178	0.141	0.142	0.142	0.131	—	6/1	17/2	17/2	24/5	38/5	38/7	38/8	40/4	41/4	38/1	37/1	37/1	39/4	41/12	41/14
26 H. chaophraya 2	0.125	0.125	0.125	0.137	0.142	0.152	0.152	0.152	0.152	0.147	0.130	0.147	0.151	0.161	0.140	0.140	0.163	0.163	0.158	0.190	0.139	0.162	0.162	0.142	0.023	—	13/3	13/3	20/5	36/6	34/8	36/8	40/5	41/5	34/1	33/1	33/1	39/4	40/12	41/15
27 H. chaophraya 3	0.134	0.134	0.134	0.130	0.134	0.157	0.157	0.157	0.157	0.139	0.118	0.151	0.152	0.157	0.152	0.152	0.145	0.145	0.141	0.163	0.135	0.127	0.127	0.155	0.066	0.055	—	0/0	23/7	36/7	36/9	41/10	36/6	37/6	34/3	35/3	35/3	34/6	38/14	43/16
28 H. chaophraya 4	0.134	0.134	0.134	0.130	0.134	0.157	0.157	0.157	0.157	0.139	0.118	0.151	0.152	0.157	0.152	0.152	0.145	0.145	0.141	0.163	0.135	0.127	0.127	0.155	0.066	0.055	0.000	—	23/7	36/7	36/9	41/10	36/6	37/6	34/3	35/3	35/3	34/6	38/14	43/16
29 H. chaophraya 6	0.173	0.172	0.172	0.172	0.177	0.179	0.179	0.179	0.179	0.179	0.132	0.173	0.167	0.178	0.131	0.131	0.168	0.168	0.161	0.186	0.105	0.165	0.165	0.164	0.111	0.093	0.115	0.115	—	31/10	27/12	36/10	35/7	36/7	28/5	27/5	27/5	34/8	35/16	36/19
30 H. walga 1	0.170	0.174	0.174	0.165	0.160	0.148	0.148	0.148	0.148	0.140	0.144	0.157	0.176	0.172	0.180	0.180	0.139	0.139	0.142	0.189	0.116	0.166	0.166	0.182	0.161	0.158	0.160	0.160	0.158	—	14/2	25/9	30/5	31/5	35/6	34/6	34/6	30/7	38/13	43/13
31 H. imbricata	0.177	0.182	0.182	0.164	0.168	0.160	0.160	0.160	0.160	0.147	0.169	0.173	0.203	0.189	0.197	0.197	0.159	0.159	0.162	0.188	0.131	0.156	0.156	0.181	0.160	0.157	0.167	0.167	0.151	0.053	—	21/11	24/7	25/7	31/8	30/8	30/8	28/9	38/13	40/13
32 H. oxyrhyncha	0.157	0.162	0.162	0.152	0.157	0.157	0.157	0.157	0.157	0.165	0.152	0.165	0.195	0.195	0.204	0.204	0.168	0.168	0.164	0.195	0.139	0.152	0.152	0.202	0.172	0.167	0.194	0.194	0.186	0.118	0.110	—	22/6	23/6	38/7	37/7	37/7	27/6	35/16	35/20
33 H. signifer 2	0.139	0.143	0.143	0.142	0.147	0.135	0.135	0.135	0.135	0.143	0.135	0.143	0.168	0.173	0.163	0.163	0.146	0.146	0.151	0.175	0.131	0.139	0.139	0.208	0.167	0.173	0.156	0.156	0.168	0.124	0.107	0.098	—	1/0	32/5	33/5	33/5	25/4	36/14	38/16
34 H. signifer 3	0.143	0.147	0.147	0.147	0.151	0.139	0.139	0.139	0.139	0.148	0.139	0.148	0.163	0.168	0.167	0.167	0.150	0.150	0.155	0.179	0.135	0.143	0.143	0.203	0.172	0.178	0.160	0.160	0.172	0.128	0.111	0.100	0.003	—	33/5	34/5	34/5	26/4	37/14	35/16
35 H. granulata 1	0.153	0.149	0.149	0.157	0.161	0.163	0.163	0.163	0.163	0.145	0.167	0.163	0.161	0.157	0.151	0.151	0.165	0.165	0.168	0.186	0.145	0.151	0.151	0.165	0.146	0.131	0.134	0.134	0.129	0.149	0.139	0.166	0.131	0.135	—	1/0	1/0	35/3	34/11	39/15
36 H. granulata 2	0.149	0.145	0.145	0.153	0.157	0.158	0.158	0.158	0.158	0.141	0.163	0.158	0.156	0.153	0.147	0.147	0.169	0.169	0.171	0.191	0.141	0.147	0.147	0.169	0.142	0.127	0.139	0.139	0.124	0.144	0.135	0.161	0.135	0.139	0.003	—	0/0	34/3	34/11	39/15
37 H. granulata 3	0.149	0.145	0.145	0.153	0.157	0.158	0.158	0.158	0.158	0.141	0.163	0.158	0.156	0.153	0.147	0.147	0.169	0.169	0.171	0.191	0.141	0.147	0.147	0.169	0.142	0.127	0.139	0.139	0.124	0.144	0.135	0.161	0.135	0.139	0.003	0.000	—	34/3	34/11	39/15
38 H. fai 2	0.130	0.130	0.130	0.125	0.130	0.098	0.098	0.098	0.098	0.114	0.139	0.101	0.138	0.151	0.179	0.179	0.145	0.145	0.149	0.168	0.106	0.102	0.102	0.209	0.163	0.165	0.147	0.147	0.169	0.133	0.132	0.124	0.101	0.105	0.139	0.135	0.135	—	33/40	32/39
39 H. pacifica	0.201	0.205	0.205	0.197	0.192	0.215	0.215	0.215	0.215	0.206	0.206	0.220	0.194	0.200	0.203	0.203	0.190	0.190	0.190	0.212	0.191	0.167	0.167	0.195	0.203	0.201	0.186	0.186	0.206	0.188	0.188	0.186	0.182	0.187	0.163	0.163	0.163	0.203	—	20/24
40 H. schmardae	0.219	0.223	0.223	0.243	0.249	0.224	0.224	0.224	0.224	0.224	0.224	0.219	0.235	0.231	0.251	0.251	0.241	0.241	0.239	0.254	0.218	0.206	0.206	0.187	0.212	0.217	0.228	0.228	0.223	0.211	0.197	0.203	0.192	0.187	0.202	0.202	0.202	0.215	0.119	—

Appendix 4.2.3a. Uncorrected 'p' distance matrix for partial 16S sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	
1	*H. uamak* 1	-
2	*H. uamak* 2	0.004	-
3	*H. uamak* 3	0.009	0.009	-
4	*H. uamak* 4	0.002	0.002	0.007	-
5	*H. uamak* 5	0.018	0.018	0.020	0.017	-
6	*H. uamak* 6	0.009	0.009	0.015	0.007	0.020	-
7	*H. uamak* 7	0.004	0.006	0.014	0.006	0.020	0.002	-
8	*H. uamak* 8	0.006	0.006	0.011	0.004	0.017	0.004	0.002	-
9	*H. uamak* 9	0.007	0.007	0.009	0.006	0.019	0.006	0.004	0.002	-
10	*H.* sp. A 1	0.026	0.028	0.031	0.024	0.030	0.028	0.026	0.024	0.028	-
11	*H.* sp. A 2	0.032	0.032	0.038	0.030	0.034	0.030	0.032	0.030	0.032	0.006	-
12	*H.* sp. A 3	0.032	0.029	0.038	0.029	0.038	0.029	0.032	0.029	0.031	0.006	0.013	-
13	*H.* sp. A 4	0.026	0.026	0.031	0.024	0.030	0.028	0.026	0.024	0.026	0.000	0.006	0.006	-
14	*H.* sp. A 6	0.022	0.020	0.028	0.020	0.030	0.024	0.020	0.020	0.022	0.026	0.032	0.034	0.026	-
15	*H.* sp. A 7	0.030	0.028	0.032	0.028	0.037	0.032	0.024	0.028	0.026	0.033	0.038	0.036	0.033	0.011	-
16	*H.* sp. A 8	0.022	0.021	0.028	0.020	0.030	0.024	0.020	0.020	0.022	0.026	0.034	0.030	0.026	0.004	0.011	-
17	*H.* sp. A 9	0.028	0.028	0.033	0.026	0.028	0.030	0.026	0.026	0.028	0.006	0.009	0.009	0.006	0.028	0.035	0.026	-
18	*H. undulata* 1	0.015	0.015	0.017	0.013	0.026	0.013	0.012	0.009	0.007	0.030	0.036	0.036	0.030	0.026	0.030	0.026	0.032	-
19	*H. undulata* 2	0.020	0.022	0.026	0.020	0.033	0.020	0.017	0.016	0.016	0.037	0.044	0.043	0.037	0.034	0.042	0.034	0.039	0.010	-
20	*H. undulata* 3	0.011	0.011	0.017	0.009	0.022	0.009	0.008	0.006	0.007	0.026	0.032	0.032	0.026	0.022	0.030	0.022	0.028	0.002	0.008	-
21	*H. gerrardi* 1	0.041	0.041	0.043	0.039	0.041	0.039	0.038	0.035	0.037	0.045	0.051	0.058	0.045	0.045	0.052	0.045	0.047	0.043	0.047	0.041	-
22	*H. gerrardi* 2	0.041	0.041	0.043	0.039	0.041	0.039	0.038	0.035	0.037	0.045	0.051	0.058	0.045	0.045	0.052	0.045	0.046	0.043	0.047	0.041	0.006	-
23	*H. gerrardi* 3	0.045	0.044	0.046	0.043	0.045	0.043	0.042	0.039	0.041	0.048	0.055	0.060	0.048	0.048	0.056	0.047	0.050	0.048	0.051	0.045	0.002	0.007	-
24	*H. gerrardi* 4	0.043	0.043	0.045	0.041	0.043	0.041	0.040	0.037	0.039	0.046	0.051	0.060	0.046	0.046	0.054	0.047	0.048	0.044	0.049	0.043	0.002	0.007	0.000	-
25	*H. gerrardi* 5	0.041	0.041	0.043	0.039	0.041	0.039	0.038	0.035	0.037	0.045	0.051	0.058	0.045	0.045	0.052	0.045	0.046	0.043	0.047	0.041	0.006	0.000	0.007	0.007	-
26	*H. gerrardi* 6	0.047	0.047	0.046	0.045	0.043	0.045	0.042	0.041	0.043	0.045	0.053	0.054	0.045	0.050	0.054	0.049	0.047	0.047	0.051	0.045	0.024	0.030	0.026	0.026	0.030	-
27	?*H. gerrardi* 7	0.048	0.048	0.050	0.047	0.045	0.047	0.044	0.043	0.045	0.047	0.053	0.058	0.047	0.052	0.060	0.052	0.048	0.048	0.053	0.047	0.032	0.028	0.034	0.034	0.028	0.011	-
28	?*H. gerrardi* 8	0.043	0.043	0.044	0.041	0.043	0.041	0.040	0.037	0.039	0.046	0.051	0.060	0.046	0.046	0.054	0.047	0.048	0.045	0.049	0.043	0.007	0.002	0.006	0.006	0.002	0.032	0.028	-
29	?*H. gerrardi* 9	0.048	0.052	0.054	0.050	0.046	0.050	0.045	0.046	0.048	0.048	0.051	0.064	0.048	0.054	0.062	0.058	0.052	0.052	0.055	0.050	0.024	0.030	0.026	0.024	0.030	0.009	0.015	0.030	-
30	?*H. gerrardi* 10	0.050	0.054	0.056	0.052	0.049	0.048	0.047	0.048	0.050	0.053	0.053	0.064	0.053	0.056	0.060	0.058	0.054	0.054	0.058	0.052	0.027	0.033	0.029	0.027	0.033	0.010	0.018	0.033	0.002	-
31	*H. toshi* 1	0.037	0.037	0.039	0.035	0.039	0.035	0.034	0.032	0.034	0.035	0.042	0.043	0.035	0.041	0.045	0.039	0.037	0.037	0.040	0.034	0.047	0.045	0.050	0.048	0.045	0.043	0.043	0.047	0.047	0.051	-
32	*H. toshi* 2	0.045	0.042	0.047	0.042	0.047	0.038	0.040	0.038	0.040	0.045	0.051	0.045	0.045	0.049	0.049	0.045	0.045	0.045	0.048	0.041	0.053	0.055	0.053	0.055	0.055	0.047	0.051	0.057	0.055	0.055	0.006	-
33	*H. pastinacoides*	0.037	0.037	0.039	0.035	0.030	0.039	0.038	0.035	0.037	0.037	0.044	0.047	0.037	0.041	0.048	0.041	0.039	0.037	0.045	0.033	0.047	0.043	0.050	0.048	0.043	0.047	0.045	0.045	0.050	0.055	0.041	0.051	-
34	*H. uarnacoides* 1	0.037	0.037	0.039	0.035	0.033	0.039	0.040	0.035	0.037	0.041	0.045	0.044	0.041	0.041	0.048	0.037	0.037	0.037	0.045	0.033	0.054	0.052	0.048	0.052	0.052	0.056	0.058	0.050	0.061	0.064	0.054	0.053	0.041	-
35	*H. uarnacoides* 2	0.035	0.035	0.037	0.033	0.031	0.037	0.038	0.033	0.035	0.039	0.043	0.042	0.039	0.039	0.046	0.035	0.035	0.035	0.043	0.032	0.052	0.050	0.046	0.050	0.050	0.054	0.056	0.048	0.059	0.062	0.052	0.051	0.043	0.002	-
36	*H.* sp. E 1	0.027	0.029	0.034	0.029	0.030	0.029	0.027	0.029	0.031	0.032	0.036	0.038	0.032	0.034	0.038	0.034	0.028	0.032	0.036	0.027	0.054	0.054	0.058	0.056	0.054	0.056	0.058	0.056	0.058	0.057	0.047	0.053	0.041	0.034	0.032	-
37	*H.* sp. E 2	0.030	0.030	0.031	0.028	0.026	0.032	0.030	0.028	0.030	0.026	0.032	0.036	0.026	0.030	0.037	0.030	0.024	0.030	0.037	0.026	0.045	0.045	0.048	0.046	0.045	0.048	0.050	0.046	0.052	0.056	0.039	0.049	0.033	0.030	0.028	0.002	-
38	*H.* sp. F	0.041	0.041	0.043	0.039	0.039	0.039	0.040	0.035	0.037	0.048	0.053	0.058	0.048	0.048	0.052	0.047	0.050	0.041	0.049	0.037	0.043	0.043	0.039	0.041	0.043	0.052	0.054	0.041	0.056	0.059	0.054	0.055	0.048	0.045	0.043	0.046	0.041	-
39	*H. chaophraya* 1	0.057	0.058	0.056	0.056	0.059	0.056	0.055	0.052	0.050	0.054	0.057	0.067	0.054	0.052	0.049	0.054	0.060	0.054	0.067	0.054	0.073	0.071	0.075	0.073	0.071	0.077	0.075	0.071	0.074	0.080	0.060	0.069	0.061	0.067	0.065	0.070	0.059	0.062	-
40	*H. chaophraya* 2	0.050	0.050	0.056	0.049	0.054	0.049	0.048	0.045	0.047	0.049	0.055	0.060	0.049	0.047	0.051	0.045	0.052	0.050	0.060	0.047	0.068	0.066	0.067	0.067	0.066	0.069	0.070	0.066	0.073	0.078	0.058	0.065	0.056	0.058	0.056	0.064	0.054	0.054	0.009	-
41	*H. chaophraya* 3	0.043	0.043	0.046	0.041	0.046	0.041	0.039	0.037	0.039	0.044	0.049	0.055	0.044	0.046	0.052	0.047	0.047	0.046	0.055	0.043	0.054	0.050	0.054	0.054	0.050	0.060	0.058	0.050	0.061	0.068	0.058	0.067	0.056	0.054	0.052	0.057	0.048	0.045	0.037	0.030	-
42	*H. chaophraya* 4	0.044	0.041	0.046	0.043	0.044	0.043	0.039	0.039	0.041	0.048	0.055	0.057	0.048	0.050	0.050	0.050	0.050	0.048	0.057	0.044	0.054	0.050	0.054	0.054	0.050	0.060	0.058	0.050	0.063	0.068	0.056	0.063	0.054	0.058	0.055	0.064	0.056	0.048	0.037	0.035	0.011	-
43	*H. chaophraya* 5	0.054	0.054	0.059	0.052	0.057	0.052	0.051	0.048	0.050	0.052	0.057	0.063	0.052	0.050	0.050	0.050	0.056	0.054	0.063	0.050	0.071	0.069	0.071	0.071	0.069	0.073	0.073	0.069	0.074	0.080	0.058	0.065	0.059	0.063	0.061	0.068	0.057	0.058	0.007	0.004	0.033	0.035	-
44	*H. chaophraya* 6	0.056	0.056	0.061	0.054	0.059	0.054	0.053	0.050	0.052	0.054	0.061	0.065	0.054	0.052	0.052	0.052	0.058	0.056	0.063	0.052	0.073	0.071	0.073	0.072	0.071	0.075	0.075	0.071	0.078	0.084	0.060	0.067	0.061	0.065	0.063	0.070	0.059	0.060	0.011	0.008	0.035	0.037	0.008	-
45	*H. walga* 1	0.052	0.052	0.054	0.050	0.050	0.051	0.050	0.047	0.049	0.054	0.059	0.064	0.054	0.048	0.056	0.045	0.052	0.050	0.060	0.047	0.058	0.056	0.058	0.058	0.056	0.060	0.060	0.056	0.064	0.068	0.052	0.059	0.056	0.053	0.050	0.061	0.052	0.058	0.073	0.065	0.064	0.067	0.069	0.071	-
46	*H. walga* 2	0.047	0.047	0.049	0.045	0.045	0.045	0.044	0.041	0.043	0.047	0.049	0.057	0.047	0.043	0.051	0.041	0.045	0.045	0.054	0.041	0.056	0.056	0.060	0.058	0.056	0.058	0.060	0.058	0.058	0.063	0.047	0.057	0.050	0.056	0.054	0.055	0.047	0.058	0.063	0.062	0.063	0.067	0.065	0.067	0.009	-
47	*H. imbricata*	0.048	0.048	0.050	0.047	0.045	0.047	0.046	0.043	0.045	0.045	0.051	0.053	0.045	0.045	0.052	0.041	0.041	0.047	0.054	0.043	0.060	0.058	0.060	0.060	0.058	0.060	0.062	0.058	0.067	0.072	0.054	0.065	0.054	0.051	0.051	0.055	0.047	0.056	0.071	0.060	0.058	0.062	0.065	0.067	0.017	0.017	-
48	*H. oxyrhyncha*	0.063	0.063	0.064	0.061	0.057	0.063	0.068	0.063	0.064	0.061	0.065	0.070	0.061	0.068	0.072	0.068	0.059	0.070	0.081	0.067	0.069	0.071	0.071	0.071	0.071	0.073	0.076	0.072	0.076	0.080	0.077	0.080	0.069	0.065	0.063	0.068	0.061	0.073	0.091	0.088	0.080	0.086	0.091	0.093	0.063	0.059	0.057	-
49	*H. signifer* 1	0.065	0.065	0.067	0.063	0.059	0.065	0.070	0.065	0.067	0.061	0.063	0.070	0.061	0.070	0.074	0.068	0.059	0.072	0.083	0.069	0.072	0.074	0.071	0.070	0.074	0.076	0.080	0.072	0.080	0.084	0.078	0.084	0.071	0.067	0.065	0.070	0.063	0.073	0.092	0.086	0.080	0.086	0.090	0.092	0.063	0.061	0.055	0.002	-
50	*H. signifer* 2	0.067	0.067	0.069	0.065	0.061	0.071	0.071	0.067	0.069	0.063	0.070	0.076	0.063	0.072	0.080	0.071	0.060	0.074	0.085	0.071	0.071	0.073	0.071	0.071	0.073	0.075	0.080	0.073	0.082	0.088	0.078	0.086	0.071	0.069	0.069	0.076	0.065	0.075	0.097	0.086	0.076	0.084	0.091	0.093	0.062	0.062	0.054	0.008	0.008	-
51	*H. signifer* 3	0.067	0.067	0.069	0.065	0.061	0.071	0.071	0.067	0.069	0.063	0.070	0.076	0.063	0.072	0.080	0.071	0.060	0.074	0.085	0.071	0.073	0.075	0.073	0.073	0.075	0.077	0.082	0.075	0.083	0.090	0.078	0.087	0.071	0.071	0.071	0.076	0.065	0.077	0.097	0.086	0.078	0.086	0.091	0.093	0.062	0.062	0.056	0.009	0.008	0.000	-
52	*H. granulata* 1	0.054	0.050	0.056	0.052	0.052	0.052	0.049	0.050	0.052	0.059	0.062	0.066	0.059	0.052	0.056	0.052	0.065	0.056	0.061	0.054	0.056	0.057	0.059	0.056	0.057	0.075	0.076	0.058	0.072	0.072	0.067	0.069	0.065	0.059	0.058	0.057	0.056	0.054	0.067	0.062	0.056	0.056	0.063	0.067	0.073	0.071	0.071	0.087	0.086	0.093	0.093	-
53	*H. granulata* 2	0.041	0.041	0.043	0.039	0.041	0.041	0.041	0.037	0.039	0.050	0.049	0.059	0.050	0.044	0.048	0.043	0.054	0.042	0.051	0.041	0.048	0.050	0.048	0.046	0.050	0.061	0.065	0.048	0.063	0.066	0.056	0.061	0.054	0.048	0.046	0.055	0.048	0.039	0.054	0.048	0.044	0.046	0.052	0.054	0.060	0.060	0.056	0.078	0.074	0.078	0.078	0.017	-
54	*H. granulata* 3	0.044	0.044	0.043	0.043	0.042	0.043	0.043	0.041	0.039	0.050	0.053	0.059	0.050	0.046	0.047	0.046	0.056	0.042	0.055	0.044	0.050	0.052	0.054	0.050	0.052	0.065	0.067	0.052	0.067	0.068	0.058	0.063	0.056	0.054	0.052	0.055	0.050	0.045	0.054	0.052	0.048	0.050	0.054	0.057	0.064	0.061	0.062	0.078	0.076	0.084	0.084	0.013	0.007	-
55	*H. fai* 1	0.033	0.037	0.037	0.035	0.033	0.035	0.029	0.031	0.033	0.037	0.044	0.047	0.037	0.037	0.045	0.035	0.035	0.033	0.036	0.029	0.053	0.053	0.053	0.053	0.053	0.057	0.059	0.053	0.057	0.062	0.045	0.054	0.045	0.031	0.029	0.018	0.018	0.043	0.063	0.053	0.049	0.057	0.057	0.059	0.053	0.051	0.045	0.074	0.075	0.075	0.075	0.057	0.053	0.057	-
56	*H. jenkinsii* 1	0.039	0.039	0.041	0.037	0.031	0.041	0.040	0.037	0.039	0.044	0.049	0.057	0.044	0.044	0.052	0.045	0.041	0.046	0.055	0.043	0.048	0.046	0.048	0.048	0.046	0.056	0.058	0.046	0.059	0.064	0.052	0.061	0.046	0.037	0.037	0.044	0.037	0.050	0.070	0.062	0.048	0.050	0.067	0.069	0.052	0.054	0.049	0.066	0.068	0.058	0.059	0.059	0.052	0.054	0.039	-
57	*H. jenkinsii* 2	0.056	0.054	0.058	0.054	0.049	0.054	0.048	0.054	0.056	0.065	0.062	0.059	0.065	0.062	0.069	0.062	0.058	0.060	0.070	0.056	0.069	0.067	0.069	0.069	0.067	0.077	0.079	0.067	0.081	0.068	0.073	0.061	0.066	0.052	0.052	0.048	0.058	0.068	0.092	0.083	0.069	0.070	0.088	0.090	0.074	0.075	0.070	0.082	0.084	0.079	0.081	0.071	0.069	0.069	0.061	0.021	-
58	*H. jenkinsii* 3	0.050	0.050	0.052	0.048	0.043	0.045	0.044	0.048	0.050	0.056	0.053	0.057	0.056	0.054	0.062	0.054	0.049	0.058	0.068	0.054	0.060	0.058	0.060	0.060	0.058	0.068	0.069	0.058	0.071	0.064	0.064	0.061	0.058	0.048	0.048	0.044	0.049	0.062	0.083	0.074	0.060	0.062	0.079	0.081	0.064	0.066	0.060	0.072	0.074	0.069	0.071	0.067	0.063	0.063	0.051	0.011	0.011	-
59	*H. pacifica*	0.093	0.091	0.095	0.091	0.087	0.093	0.091	0.089	0.091	0.089	0.091	0.100	0.089	0.089	0.097	0.086	0.090	0.098	0.111	0.095	0.086	0.088	0.080	0.084	0.088	0.082	0.088	0.088	0.082	0.088	0.097	0.098	0.095	0.097	0.095	0.104	0.093	0.077	0.106	0.103	0.091	0.095	0.108	0.110	0.086	0.086	0.085	0.105	0.105	0.105	0.107	0.101	0.093	0.095	0.098	0.089	0.107	0.100	-
60	*H. schmardae*	0.093	0.092	0.095	0.092	0.082	0.094	0.091	0.089	0.092	0.093	0.097	0.111	0.093	0.091	0.099	0.093	0.096	0.095	0.105	0.091	0.092	0.094	0.092	0.090	0.094	0.089	0.092	0.092	0.088	0.093	0.099	0.106	0.092	0.094	0.093	0.100	0.090	0.090	0.106	0.103	0.088	0.090	0.106	0.110	0.091	0.088	0.087	0.109	0.110	0.109	0.111	0.103	0.095	0.101	0.097	0.084	0.100	0.094	0.060	-

Appendix 4.2.3b. Uncorrected 'p' distance matrix for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-																																							
2	*H. uarnak* 2	0.003	-																																						
3	*H. uarnak* 3	0.003	0.000	-																																					
4	*H. uarnak* 6	0.041	0.044	0.044	-																																				
5	*H. uarnak* 8	0.044	0.047	0.047	0.009	-																																			
6	*H.* sp. A 1	0.075	0.079	0.079	0.079	0.082	-																																		
7	*H.* sp. A 2	0.075	0.079	0.079	0.079	0.082	0.000	-																																	
8	*H.* sp. A 4	0.075	0.079	0.079	0.079	0.082	0.000	0.000	-																																
9	*H.* sp. A 5	0.075	0.079	0.079	0.079	0.082	0.000	0.000	0.000	-																															
10	*H.* sp. A 6	0.075	0.079	0.079	0.075	0.079	0.044	0.044	0.044	0.044	-																														
11	*H.* sp. A 7	0.091	0.094	0.094	0.094	0.097	0.085	0.085	0.085	0.085	0.072	-																													
12	*H.* sp. A 9	0.075	0.072	0.072	0.085	0.088	0.013	0.013	0.013	0.013	0.044	0.091	-																												
13	*H. undulata* 2	0.067	0.067	0.067	0.067	0.064	0.090	0.090	0.090	0.090	0.083	0.093	0.093	-																											
14	*H. undulata* 3	0.064	0.064	0.064	0.064	0.061	0.093	0.093	0.093	0.093	0.068	0.096	0.090	0.016	-																										
15	*H. gerrardi* 1	0.129	0.126	0.126	0.132	0.129	0.138	0.138	0.138	0.138	0.138	0.132	0.132	0.134	0.132	-																									
16	*H. gerrardi* 5	0.129	0.126	0.126	0.132	0.129	0.138	0.138	0.138	0.138	0.138	0.132	0.132	0.134	0.132	0.000	-																								
17	*H. toshi* 1	0.135	0.132	0.132	0.120	0.116	0.123	0.123	0.123	0.123	0.129	0.116	0.116	0.141	0.132	0.094	0.094	-																							
18	*H. toshi* 2	0.135	0.132	0.132	0.120	0.116	0.123	0.123	0.123	0.123	0.129	0.116	0.116	0.141	0.132	0.094	0.094	0.000	-																						
19	*H. toshi* 3	0.143	0.139	0.139	0.127	0.124	0.130	0.130	0.130	0.130	0.136	0.124	0.124	0.144	0.138	0.101	0.101	0.006	0.006	-																					
20	*H. pastinacoides*	0.138	0.142	0.142	0.126	0.132	0.142	0.142	0.142	0.142	0.135	0.110	0.142	0.164	0.154	0.120	0.120	0.107	0.107	0.114	-																				
21	*H. uarnacoides* 1	0.120	0.123	0.123	0.126	0.123	0.104	0.104	0.104	0.104	0.116	0.094	0.104	0.122	0.125	0.123	0.123	0.104	0.104	0.108	0.132	-																			
22	*H.* sp. E 1	0.116	0.120	0.120	0.104	0.107	0.135	0.135	0.135	0.135	0.116	0.113	0.142	0.131	0.129	0.129	0.129	0.123	0.123	0.130	0.120	0.116	-																		
23	*H.* sp. E 2	0.116	0.120	0.120	0.104	0.107	0.135	0.135	0.135	0.135	0.116	0.113	0.142	0.131	0.129	0.129	0.129	0.123	0.123	0.130	0.120	0.116	0.000	-																	
24	*H.* sp. F	0.167	0.170	0.170	0.158	0.167	0.167	0.167	0.167	0.167	0.164	0.145	0.174	0.170	0.161	0.177	0.177	0.174	0.174	0.174	0.167	0.161	0.133	0.133	-																
25	*H. chaophraya* 1	0.120	0.120	0.120	0.126	0.129	0.139	0.139	0.139	0.139	0.133	0.117	0.135	0.140	0.143	0.142	0.142	0.145	0.145	0.142	0.152	0.123	0.123	0.123	0.117	-															
26	*H. chaophraya* 2	0.111	0.111	0.111	0.121	0.124	0.131	0.131	0.131	0.131	0.128	0.115	0.127	0.131	0.138	0.124	0.124	0.141	0.141	0.137	0.161	0.122	0.138	0.138	0.125	0.023	-														
27	*H. chaophraya* 3	0.119	0.118	0.118	0.116	0.119	0.135	0.135	0.135	0.135	0.122	0.106	0.131	0.132	0.136	0.134	0.134	0.128	0.128	0.125	0.142	0.119	0.112	0.112	0.136	0.062	0.052	-													
28	*H. chaophraya* 4	0.119	0.118	0.118	0.116	0.119	0.135	0.135	0.135	0.135	0.122	0.106	0.131	0.132	0.136	0.134	0.134	0.128	0.128	0.125	0.142	0.119	0.112	0.112	0.136	0.062	0.052	0.000	-												
29	*H. chaophraya* 6	0.148	0.148	0.148	0.149	0.152	0.152	0.152	0.152	0.152	0.153	0.117	0.148	0.144	0.152	0.117	0.117	0.144	0.144	0.141	0.159	0.096	0.142	0.142	0.143	0.100	0.086	0.104	0.104	-											
30	*H. walga* 1	0.146	0.149	0.149	0.143	0.139	0.130	0.130	0.130	0.130	0.123	0.127	0.136	0.151	0.148	0.155	0.155	0.123	0.123	0.127	0.161	0.105	0.142	0.142	0.155	0.139	0.137	0.138	0.138	0.137	-										
31	*H. imbricata*	0.152	0.155	0.155	0.142	0.146	0.139	0.139	0.139	0.139	0.130	0.146	0.149	0.170	0.161	0.168	0.168	0.139	0.139	0.142	0.161	0.117	0.136	0.136	0.155	0.139	0.137	0.145	0.145	0.134	0.051	-									
32	*H. oxyrhyncha*	0.136	0.140	0.140	0.133	0.136	0.136	0.136	0.136	0.136	0.143	0.133	0.143	0.163	0.164	0.171	0.171	0.146	0.146	0.142	0.165	0.124	0.133	0.133	0.171	0.148	0.144	0.164	0.164	0.159	0.108	0.101	-								
33	*H. signifer* 2	0.123	0.126	0.126	0.126	0.129	0.120	0.120	0.120	0.120	0.126	0.120	0.126	0.144	0.148	0.142	0.142	0.129	0.129	0.133	0.151	0.116	0.123	0.123	0.174	0.143	0.147	0.135	0.135	0.144	0.111	0.098	0.089	-							
34	*H. signifer* 3	0.126	0.129	0.129	0.129	0.132	0.123	0.123	0.123	0.123	0.129	0.123	0.129	0.141	0.145	0.145	0.145	0.132	0.132	0.136	0.154	0.120	0.126	0.126	0.170	0.146	0.150	0.138	0.138	0.148	0.114	0.101	0.092	0.003	-						
35	*H. granulata* 1	0.132	0.129	0.129	0.135	0.138	0.138	0.138	0.138	0.138	0.126	0.142	0.138	0.138	0.135	0.132	0.132	0.142	0.142	0.143	0.157	0.126	0.129	0.129	0.142	0.126	0.115	0.118	0.118	0.114	0.130	0.124	0.143	0.116	0.120	-					
36	*H. granulata* 2	0.129	0.126	0.126	0.132	0.135	0.135	0.135	0.135	0.135	0.123	0.138	0.135	0.134	0.132	0.129	0.129	0.145	0.145	0.146	0.160	0.123	0.126	0.126	0.145	0.123	0.111	0.121	0.121	0.111	0.127	0.120	0.140	0.120	0.123	0.003	-				
37	*H. granulata* 3	0.129	0.126	0.126	0.132	0.135	0.135	0.135	0.135	0.135	0.123	0.138	0.135	0.134	0.132	0.129	0.129	0.145	0.145	0.146	0.160	0.123	0.126	0.126	0.145	0.123	0.111	0.121	0.121	0.111	0.127	0.120	0.140	0.120	0.123	0.003	0.000	-			
38	*H. fai* 2	0.115	0.115	0.115	0.112	0.115	0.089	0.089	0.089	0.089	0.102	0.121	0.092	0.122	0.131	0.153	0.153	0.127	0.127	0.131	0.144	0.096	0.093	0.093	0.173	0.139	0.141	0.129	0.129	0.145	0.118	0.118	0.112	0.092	0.096	0.121	0.118	0.118	-		
39	*H. pacifica*	0.171	0.174	0.174	0.167	0.164	0.180	0.180	0.180	0.180	0.174	0.174	0.183	0.166	0.170	0.174	0.174	0.164	0.164	0.164	0.180	0.164	0.145	0.145	0.167	0.171	0.170	0.160	0.160	0.175	0.161	0.161	0.161	0.158	0.161	0.142	0.142	0.142	0.172	-	
40	*H. schmardae*	0.185	0.188	0.188	0.200	0.204	0.188	0.188	0.188	0.188	0.188	0.188	0.184	0.196	0.193	0.206	0.206	0.200	0.200	0.200	0.210	0.184	0.175	0.175	0.162	0.178	0.182	0.190	0.190	0.188	0.177	0.168	0.174	0.165	0.162	0.172	0.172	0.172	0.182	0.108	-

Appendix 4.2.4a. HKY85 distance matrix at first codon for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-																																							
2	*H. uarnak* 2	0.009	-																																						
3	*H. uarnak* 3	0.009	0.000	-																																					
4	*H. uarnak* 6	0.019	0.028	0.028	-																																				
5	*H. uarnak* 8	0.009	0.019	0.019	0.009	-																																			
6	*H.* sp. A 1	0.028	0.038	0.038	0.047	0.038	-																																		
7	*H.* sp. A 2	0.028	0.038	0.038	0.047	0.038	0.000	-																																	
8	*H.* sp. A 4	0.028	0.038	0.038	0.047	0.038	0.000	0.000	-																																
9	*H.* sp. A 5	0.028	0.038	0.038	0.047	0.038	0.000	0.000	0.000	-																															
10	*H.* sp. A 6	0.047	0.057	0.057	0.047	0.038	0.038	0.038	0.038	0.038	-																														
11	*H.* sp. A 7	0.038	0.047	0.047	0.057	0.047	0.047	0.047	0.047	0.047	0.047	-																													
12	*H.* sp. A 9	0.038	0.028	0.028	0.057	0.047	0.009	0.009	0.009	0.009	0.047	0.057	-																												
13	*H. undulata* 2	0.019	0.019	0.019	0.038	0.029	0.048	0.048	0.048	0.048	0.048	0.039	0.048	-																											
14	*H. undulata* 3	0.029	0.029	0.029	0.028	0.019	0.057	0.057	0.057	0.057	0.038	0.048	0.058	0.010	-																										
15	*H. gerrardi* 1	0.075	0.066	0.066	0.075	0.066	0.104	0.104	0.104	0.104	0.085	0.075	0.094	0.067	0.057	-																									
16	*H. gerrardi* 5	0.075	0.066	0.066	0.075	0.066	0.104	0.104	0.104	0.104	0.085	0.075	0.094	0.067	0.057	0.000	-																								
17	*H. toshi* 1	0.075	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.075	0.068	0.058	0.038	0.038	-																							
18	*H. toshi* 2	0.075	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.075	0.068	0.058	0.038	0.038	0.000	-																						
19	*H. toshi* 3	0.076	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.076	0.068	0.058	0.038	0.038	0.000	0.000	-																					
20	*H. pastinacoides*	0.075	0.085	0.085	0.066	0.066	0.104	0.104	0.104	0.104	0.085	0.057	0.113	0.077	0.067	0.057	0.057	0.038	0.038	0.038	-																				
21	*H. uarnacoides* 1	0.066	0.075	0.075	0.085	0.075	0.057	0.057	0.057	0.057	0.057	0.028	0.068	0.057	0.066	0.085	0.085	0.047	0.047	0.038	0.066	-																			
22	*H.* sp. E 1	0.085	0.094	0.094	0.085	0.075	0.094	0.094	0.094	0.094	0.075	0.066	0.104	0.088	0.078	0.094	0.094	0.075	0.075	0.076	0.075	0.066	-																		
23	*H.* sp. E 2	0.085	0.094	0.094	0.085	0.075	0.094	0.094	0.094	0.094	0.075	0.066	0.104	0.088	0.078	0.094	0.094	0.075	0.075	0.076	0.075	0.066	0.000	-																	
24	*H.* sp. F	0.086	0.096	0.096	0.067	0.076	0.115	0.115	0.115	0.115	0.105	0.096	0.124	0.097	0.087	0.124	0.124	0.105	0.105	0.105	0.095	0.104	0.077	0.077	-																
25	*H. chaophraya* 1	0.098	0.097	0.097	0.098	0.088	0.088	0.088	0.088	0.088	0.088	0.078	0.087	0.116	0.107	0.116	0.116	0.078	0.078	0.078	0.108	0.068	0.078	0.078	0.069	-															
26	*H. chaophraya* 2	0.091	0.089	0.089	0.101	0.091	0.080	0.080	0.080	0.080	0.090	0.070	0.079	0.109	0.109	0.119	0.119	0.079	0.079	0.079	0.111	0.059	0.081	0.081	0.072	0.020	-														
27	*H. chaophraya* 3	0.098	0.096	0.096	0.098	0.088	0.088	0.088	0.088	0.088	0.069	0.059	0.086	0.097	0.087	0.096	0.096	0.058	0.058	0.058	0.089	0.050	0.059	0.059	0.079	0.039	0.039	-													
28	*H. chaophraya* 4	0.098	0.096	0.096	0.098	0.088	0.088	0.088	0.088	0.088	0.069	0.059	0.086	0.097	0.087	0.096	0.096	0.058	0.058	0.058	0.089	0.050	0.059	0.059	0.079	0.039	0.039	0.000	-												
29	*H. chaophraya* 6	0.076	0.074	0.074	0.077	0.077	0.075	0.075	0.075	0.075	0.098	0.053	0.074	0.095	0.097	0.083	0.083	0.062	0.062	0.062	0.084	0.062	0.087	0.087	0.088	0.065	0.053	0.064	0.064	-											
30	*H. walga* 1	0.076	0.086	0.086	0.075	0.066	0.066	0.066	0.066	0.066	0.028	0.057	0.076	0.077	0.067	0.095	0.095	0.057	0.057	0.057	0.076	0.038	0.076	0.076	0.105	0.089	0.091	0.069	0.069	0.096	-										
31	*H. imbricata*	0.085	0.095	0.095	0.085	0.075	0.076	0.076	0.076	0.076	0.038	0.067	0.085	0.087	0.077	0.104	0.104	0.067	0.067	0.067	0.085	0.047	0.085	0.085	0.114	0.098	0.101	0.079	0.079	0.106	0.010	-									
32	*H. oxyrhyncha*	0.086	0.095	0.095	0.085	0.076	0.095	0.095	0.095	0.095	0.076	0.048	0.105	0.087	0.077	0.067	0.067	0.048	0.048	0.048	0.066	0.048	0.076	0.076	0.095	0.079	0.081	0.079	0.079	0.064	0.067	0.076	-								
33	*H. signifer* 2	0.066	0.075	0.075	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.085	0.068	0.058	0.066	0.066	0.047	0.047	0.047	0.066	0.057	0.085	0.085	0.095	0.098	0.101	0.079	0.079	0.063	0.047	0.057	0.038	-							
34	*H. signifer* 3	0.066	0.075	0.075	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.085	0.068	0.058	0.066	0.066	0.047	0.047	0.047	0.066	0.057	0.085	0.085	0.095	0.098	0.101	0.079	0.079	0.063	0.047	0.057	0.038	0.000	-						
35	*H. granulata* 1	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	-					
36	*H. granulata* 2	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	0.000	-				
37	*H. granulata* 3	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	0.000	0.000	-			
38	*H. fai* 2	0.078	0.076	0.076	0.077	0.068	0.067	0.067	0.067	0.067	0.048	0.058	0.067	0.077	0.067	0.066	0.066	0.048	0.048	0.048	0.078	0.039	0.058	0.058	0.127	0.088	0.089	0.068	0.068	0.095	0.059	0.068	0.059	0.068	0.068	0.067	0.067	0.067	-		
39	*H. pacifica*	0.086	0.096	0.096	0.086	0.076	0.115	0.115	0.115	0.115	0.096	0.086	0.124	0.087	0.077	0.096	0.096	0.077	0.077	0.076	0.076	0.094	0.058	0.058	0.076	0.118	0.120	0.098	0.098	0.109	0.095	0.105	0.105	0.086	0.086	0.057	0.057	0.057	0.117	-	
40	*H. schmardae*	0.077	0.086	0.086	0.076	0.067	0.105	0.105	0.105	0.105	0.105	0.115	0.115	0.097	0.087	0.124	0.124	0.125	0.125	0.124	0.124	0.123	0.096	0.096	0.067	0.098	0.089	0.118	0.118	0.097	0.124	0.133	0.114	0.115	0.115	0.096	0.096	0.096	0.127	0.076	-

Appendix 4.2.4b. HKY85 distance matrix at second codon for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-
2	*H. uarnak* 2	0.000	-
3	*H. uarnak* 3	0.000	0.000	-
4	*H. uarnak* 6	0.000	0.000	0.000	-
5	*H. uarnak* 8	0.010	0.010	0.010	0.010	-
6	*H.* sp. A 1	0.000	0.000	0.000	0.000	0.010	-
7	*H.* sp. A 2	0.000	0.000	0.000	0.000	0.010	0.000	-
8	*H.* sp. A 4	0.000	0.000	0.000	0.000	0.010	0.000	0.000	-
9	*H.* sp. A 5	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	-
10	*H.* sp. A 6	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	-
11	*H.* sp. A 7	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	-
12	*H.* sp. A 9	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	-
13	*H. undulata* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
14	*H. undulata* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
15	*H. gerrardi* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
16	*H. gerrardi* 5	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
17	*H. toshi* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
18	*H. toshi* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
19	*H. toshi* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
20	*H. pastinacoides*	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	-
21	*H. uarnacoides* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	-
22	*H.* sp. E 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	-
23	*H.* sp. E 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	-
24	*H.* sp. F	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	-
25	*H. chaophraya* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	-
26	*H. chaophraya* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	-
27	*H. chaophraya* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	-
28	*H. chaophraya* 4	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
29	*H. chaophraya* 6	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
30	*H. walga* 1	0.010	0.010	0.010	0.010	0.020	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.020	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	-
31	*H. imbricata*	0.010	0.010	0.010	0.010	0.020	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.020	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.000	-
32	*H. oxyrhyncha*	0.020	0.020	0.020	0.020	0.030	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.019	0.019	0.020	0.020	0.020	0.020	0.019	0.030	0.020	0.020	0.020	0.029	0.019	0.019	0.019	0.019	0.019	0.030	0.030	-
33	*H. signifer* 2	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.010	0.010	0.020	-
34	*H. signifer* 3	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.010	0.010	0.020	0.000	-
35	*H. granulata* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.020	0.019	0.019	-	-
36	*H. granulata* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.020	0.019	0.019	0.000	0.000	-
37	*H. granulata* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.020	0.019	0.019	0.000	0.000	0.000	-
38	*H. fai* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.019	0.019	0.019	0.000	0.010	0.010	0.010
39	*H. pacifica*	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.011	0.020	0.020	0.030	0.029	0.029	0.010	0.040	0.040	0.040	0.029	-
40	*H. schmardae*	0.040	0.040	0.040	0.040	0.050	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.040	0.039	0.050	0.040	0.040	0.040	0.049	0.040	0.040	0.040	0.040	0.041	0.029	0.029	0.039	0.019	0.019	0.040	0.040	0.040	0.040	0.029	-

Appendix 4.2.4c. HKY85 distance matrix at third codon for partial cytochrome *b* sequences. Undefined distances (generated by PAUP) are marked with an asterisk (*)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	34	35	36	37	38	39	40
1 *H. uarnak* 1	-																																						
2 *H. uarnak* 2	0.000	-																																					
3 *H. uarnak* 3	0.000	0.000	-																																				
4 *H. uarnak* 6	0.119	0.119	0.119	-																																			
5 *H. uarnak* 8	0.131	0.131	0.131	0.010	-																																		
6 *H.* sp. A 1	0.270	0.270	0.270	0.247	0.264	-																																	
7 *H.* sp. A 2	0.270	0.270	0.270	0.247	0.264	0.000	-																																
8 *H.* sp. A 4	0.270	0.270	0.270	0.247	0.264	0.000	0.000	-																															
9 *H.* sp. A 5	0.270	0.270	0.270	0.247	0.264	0.000	0.000	0.000	-																														
10 *H.* sp. A 6	0.236	0.236	0.236	0.231	0.248	0.108	0.108	0.108	0.108	-																													
11 *H.* sp. A 7	0.350	0.350	0.350	0.321	0.342	0.294	0.294	0.294	0.294	0.224	-																												
12 *H.* sp. A 9	0.254	0.254	0.254	0.266	0.285	0.029	0.029	0.029	0.029	0.096	0.319	-																											
13 *H. undulata* 2	0.245	0.245	0.245	0.203	0.187	0.318	0.318	0.318	0.318	0.278	0.360	0.340	-																										
14 *H. undulata* 3	0.212	0.212	0.212	0.204	0.188	0.321	0.321	0.321	0.321	0.210	0.364	0.301	0.041	-																									
15 *H. gerrardi* 1	0.552	0.552	0.552	0.571	0.534	0.572	0.572	0.572	0.572	0.680	0.607	0.549	0.671	0.684	-																								
16 *H. gerrardi* 5	0.552	0.552	0.552	0.571	0.534	0.572	0.572	0.572	0.572	0.680	0.607	0.549	0.671	0.684	0.000	-																							
17 *H. toshi* 1	0.621	0.621	0.621	0.439	0.412	0.463	0.463	0.463	0.463	0.617	0.558	0.442	0.738	0.649	0.375	0.375	-																						
18 *H. toshi* 2	0.621	0.621	0.621	0.439	0.412	0.463	0.463	0.463	0.463	0.617	0.558	0.442	0.738	0.649	0.375	0.375	0.000	-																					
19 *H. toshi* 3	0.709	0.709	0.709	0.489	0.459	0.519	0.519	0.519	0.519	0.708	0.631	0.497	0.802	0.755	0.421	0.421	0.019	0.019	-																				
20 *H. pastinacoides*	0.609	0.609	0.609	0.492	0.522	0.522	0.522	0.522	0.522	0.530	0.387	0.500	1.131	0.947	0.484	0.484	0.424	0.424	0.472	-																			
21 *H. uarnacoides* 1	0.519	0.519	0.519	0.503	0.471	0.409	0.409	0.409	0.409	0.548	0.407	0.389	0.578	0.587	0.467	0.467	0.406	0.406	0.455	0.554	-																		
22 *H.* sp. E 1	0.423	0.423	0.423	0.319	0.339	0.615	0.615	0.615	0.615	0.474	0.462	0.692	0.583	0.593	0.498	0.498	0.491	0.491	0.553	0.408	0.498	-																	
23 *H.* sp. E 2	0.423	0.423	0.423	0.319	0.339	0.615	0.615	0.615	0.615	0.474	0.462	0.692	0.583	0.593	0.498	0.498	0.491	0.491	0.553	0.408	0.498	0.000	-																
24 *H.* sp. F	4.093	4.093	4.093	1.328	1.780	1.118	1.118	1.118	1.118	1.260	0.684	1.768	1.655	1.126	1.375	1.375	1.516	1.516	1.588	0.847	1.070	0.576	0.576	-															
25 *H. chaophraya* 1	0.428	0.428	0.428	0.476	0.510	0.732	0.732	0.732	0.732	0.642	0.467	0.701	0.536	0.631	0.579	0.579	0.833	0.833	0.752	0.635	0.590	0.582	0.582	0.446	-														
26 *H. chaophraya* 2	0.391	0.391	0.391	0.435	0.466	0.662	0.662	0.662	0.662	0.582	0.490	0.633	0.489	0.572	0.403	0.403	0.748	0.748	0.680	0.778	0.629	0.915	0.915	0.545	0.052	-													
27 *H. chaophraya* 3	0.419	0.419	0.419	0.384	0.410	0.659	0.659	0.659	0.659	0.578	0.427	0.626	0.525	0.614	0.562	0.562	0.630	0.630	0.577	0.580	0.631	0.525	0.525	0.643	0.187	0.142	-												
28 *H. chaophraya* 4	0.419	0.419	0.419	0.384	0.410	0.659	0.659	0.659	0.659	0.578	0.427	0.626	0.525	0.614	0.562	0.562	0.630	0.630	0.577	0.580	0.631	0.525	0.525	0.643	0.187	0.142	*8.18524	-											
29 *H. chaophraya* 6	1.138	1.138	1.138	1.042	1.029	1.213	1.213	1.213	1.213	0.975	0.569	1.144	0.718	0.881	0.422	0.422	0.900	0.900	0.807	0.831	0.322	0.842	0.842	0.669	0.353	0.284	0.389	0.389	-										
30 *H. walga* 1	0.713	0.713	0.713	0.637	0.593	0.552	0.552	0.552	0.552	0.655	0.548	0.610	0.795	0.812	0.741	0.741	0.478	0.478	0.502	0.801	0.397	0.763	0.763	0.811	0.677	0.621	0.836	0.836	0.524	-									
31 *H. imbricata*	0.732	0.732	0.732	0.571	0.610	0.608	0.608	0.608	0.608	0.671	0.755	0.732	1.320	1.021	0.912	0.912	0.596	0.596	0.630	0.712	0.467	0.566	0.566	0.681	0.587	0.544	0.857	0.857	0.439	0.178	-								
32 *H. oxyrhyncha*	0.532	0.532	0.532	0.482	0.513	0.486	0.486	0.486	0.486	0.663	0.632	0.534	1.138	1.518	*8.18524	*8.18524	0.793	0.793	0.793	0.969	0.517	0.556	0.556	1.074	0.782	0.700	2.805	2.805	1.156	0.311	0.249	-							
33 *H. signifer* 2	0.441	0.441	0.441	0.457	0.485	0.400	0.400	0.400	0.400	0.524	0.480	0.433	0.688	0.823	0.628	0.628	0.542	0.542	0.570	0.646	0.423	0.418	0.418	1.556	0.649	0.707	0.633	0.633	0.790	0.459	0.318	0.274							
34 *H. signifer* 3	0.470	0.470	0.470	0.487	0.517	0.427	0.427	0.427	0.427	0.564	0.513	0.464	0.644	0.764	0.679	0.679	0.580	0.580	0.611	0.692	0.452	0.448	0.448	1.240	0.710	0.777	0.690	0.690	0.884	0.493	0.341	0.294	-						
35 *H. granulata* 1	0.737	0.737	0.737	0.770	0.846	0.850	0.850	0.850	0.850	0.738	1.573	1.051	0.994	1.028	0.646	0.646	1.457	1.457	1.525	0.992	0.666	0.902	0.902	0.825	0.744	0.551	*8.18524	*8.18524	0.567	0.696	0.514	0.841	0.532	-					
36 *H. granulata* 2	0.675	0.675	0.675	0.703	0.767	0.766	0.766	0.766	0.766	0.669	1.225	0.907	0.873	0.895	0.594	0.594	2.181	2.181	*8.18524	1.105	0.610	0.798	0.798	0.933	0.669	0.505	*8.18524	*8.18524	0.518	0.634	0.478	0.747	0.571	0.010	-				
37 *H. granulata* 3	0.675	0.675	0.675	0.703	0.767	0.766	0.766	0.766	0.766	0.669	1.225	0.907	0.873	0.895	0.594	0.594	2.181	2.181	*8.18524	1.105	0.610	0.798	0.798	0.933	0.669	0.505	*8.18524	*8.18524	0.518	0.634	0.478	0.747	0.571	0.010	0.000	-			
38 *H. fai* 2	0.398	0.398	0.398	0.367	0.390	0.260	0.260	0.260	0.260	0.386	0.521	0.280	0.460	0.599	0.955	0.955	0.585	0.585	0.618	0.613	0.357	0.307	0.307	1.075	0.722	0.779	0.664	0.664	0.736	0.445	0.407	0.368	0.262	0.543	0.505	0.505	-		
39 *H. pacifica*	1.080	1.080	1.080	1.023	0.905	1.255	1.255	1.255	1.255	1.515	1.418	1.668	0.952	1.420	1.059	1.059	0.901	0.901	0.885	1.095	0.859	0.800	0.800	1.164	0.950	0.931	*8.18524	*8.18524	1.079	0.859	0.804	0.658	0.754	0.770	0.761	0.761	0.819	-	
40 *H. schmardae*	1.598	1.598	1.598	*8.18524	*8.18524	1.287	1.287	1.287	1.287	1.720	1.013	1.076	*8.18524	*8.18524	*8.18524	*8.18524	1.453	1.453	1.428	1.242	0.844	1.006	1.006	0.787	1.238	*8.18524	2.114	2.114	1.717	*8.18524	0.833	0.796	0.692	0.951	0.925	0.925	0.716	0.305	-

Appendix 4.2.5a. Uncorrected 'p' distance matrix at first codon for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-																																							
2	*H. uarnak* 2	0.009	-																																						
3	*H. uarnak* 3	0.009	0.000	-																																					
4	*H. uarnak* 6	0.019	0.028	0.028	-																																				
5	*H. uarnak* 8	0.009	0.019	0.019	0.009	-																																			
6	*H.* sp. A 1	0.028	0.038	0.038	0.047	0.038	-																																		
7	*H.* sp. A 2	0.028	0.038	0.038	0.047	0.038	0.000	-																																	
8	*H.* sp. A 4	0.028	0.038	0.038	0.047	0.038	0.000	0.000	-																																
9	*H.* sp. A 5	0.028	0.038	0.038	0.047	0.038	0.000	0.000	0.000	-																															
10	*H.* sp. A 6	0.047	0.057	0.057	0.047	0.038	0.038	0.038	0.038	0.038	-																														
11	*H.* sp. A 7	0.038	0.047	0.047	0.057	0.047	0.047	0.047	0.047	0.047	0.047	-																													
12	*H.* sp. A 9	0.038	0.028	0.028	0.057	0.047	0.009	0.009	0.009	0.009	0.047	0.057	-																												
13	*H. undulata* 2	0.019	0.019	0.019	0.038	0.029	0.048	0.048	0.048	0.048	0.048	0.039	0.048	-																											
14	*H. undulata* 3	0.029	0.029	0.029	0.028	0.019	0.057	0.057	0.057	0.057	0.038	0.048	0.058	0.010	-																										
15	*H. gerrardi* 1	0.075	0.066	0.066	0.075	0.066	0.104	0.104	0.104	0.104	0.085	0.075	0.094	0.067	0.057	-																									
16	*H. gerrardi* 5	0.075	0.066	0.066	0.075	0.066	0.104	0.104	0.104	0.104	0.085	0.075	0.094	0.067	0.057	0.000	-																								
17	*H. toshi* 1	0.075	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.075	0.068	0.058	0.038	0.038	-																							
18	*H. toshi* 2	0.075	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.075	0.068	0.058	0.038	0.038	0.000	-																						
19	*H. toshi* 3	0.076	0.066	0.066	0.075	0.066	0.085	0.085	0.085	0.085	0.066	0.038	0.076	0.068	0.058	0.038	0.038	0.000	0.000	-																					
20	*H. pastinacoides*	0.075	0.085	0.085	0.066	0.066	0.104	0.104	0.104	0.104	0.085	0.057	0.113	0.077	0.067	0.057	0.057	0.038	0.038	0.038	-																				
21	*H. uarnacoides* 1	0.066	0.075	0.075	0.085	0.075	0.057	0.057	0.057	0.057	0.057	0.028	0.066	0.057	0.066	0.085	0.085	0.047	0.047	0.038	0.066	-																			
22	*H.* sp. E 1	0.085	0.094	0.094	0.085	0.075	0.094	0.094	0.094	0.094	0.075	0.066	0.104	0.088	0.078	0.094	0.094	0.075	0.075	0.076	0.075	0.066	-																		
23	*H.* sp. E 2	0.085	0.094	0.094	0.085	0.075	0.094	0.094	0.094	0.094	0.075	0.066	0.104	0.088	0.078	0.094	0.094	0.075	0.075	0.076	0.075	0.066	0.000	-																	
24	*H.* sp. F	0.086	0.096	0.096	0.067	0.076	0.115	0.115	0.115	0.115	0.105	0.096	0.124	0.097	0.087	0.124	0.124	0.105	0.105	0.105	0.095	0.104	0.077	0.077	-																
25	*H. chaophraya* 1	0.098	0.097	0.097	0.098	0.088	0.088	0.088	0.088	0.088	0.088	0.078	0.087	0.116	0.107	0.116	0.116	0.078	0.078	0.078	0.108	0.068	0.078	0.078	0.069	-															
26	*H. chaophraya* 2	0.091	0.089	0.089	0.101	0.091	0.080	0.080	0.080	0.080	0.090	0.070	0.079	0.109	0.109	0.119	0.119	0.079	0.079	0.079	0.111	0.059	0.081	0.081	0.072	0.020	-														
27	*H. chaophraya* 3	0.098	0.096	0.096	0.098	0.088	0.088	0.088	0.088	0.088	0.069	0.059	0.086	0.097	0.087	0.096	0.096	0.058	0.058	0.058	0.089	0.050	0.059	0.059	0.079	0.039	0.039	-													
28	*H. chaophraya* 4	0.098	0.096	0.096	0.098	0.088	0.088	0.088	0.088	0.088	0.069	0.059	0.086	0.097	0.087	0.096	0.096	0.058	0.058	0.058	0.089	0.050	0.059	0.059	0.079	0.039	0.039	0.000	-												
29	*H. chaophraya* 6	0.076	0.074	0.074	0.077	0.077	0.075	0.075	0.075	0.075	0.096	0.053	0.074	0.095	0.097	0.083	0.083	0.062	0.062	0.062	0.084	0.062	0.087	0.087	0.088	0.065	0.053	0.064	0.064	-											
30	*H. walga* 1	0.076	0.086	0.086	0.075	0.066	0.066	0.066	0.066	0.066	0.028	0.057	0.076	0.077	0.067	0.095	0.095	0.057	0.057	0.057	0.076	0.038	0.076	0.076	0.105	0.089	0.091	0.069	0.069	0.096	-										
31	*H. imbricata*	0.085	0.095	0.095	0.085	0.075	0.076	0.076	0.076	0.076	0.038	0.067	0.085	0.087	0.077	0.104	0.104	0.067	0.067	0.067	0.085	0.047	0.085	0.085	0.114	0.098	0.101	0.079	0.079	0.106	0.010	-									
32	*H. oxyrhyncha*	0.086	0.095	0.095	0.085	0.076	0.095	0.095	0.095	0.095	0.076	0.048	0.105	0.087	0.077	0.067	0.067	0.048	0.048	0.048	0.068	0.048	0.076	0.076	0.095	0.079	0.081	0.079	0.079	0.064	0.067	0.076	-								
33	*H. signifer* 2	0.066	0.075	0.075	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.085	0.068	0.058	0.066	0.066	0.047	0.047	0.047	0.066	0.057	0.085	0.085	0.095	0.098	0.101	0.079	0.079	0.063	0.047	0.057	0.038	-							
34	*H. signifer* 3	0.066	0.075	0.075	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.085	0.068	0.058	0.066	0.066	0.047	0.047	0.047	0.066	0.057	0.085	0.085	0.095	0.098	0.101	0.079	0.079	0.063	0.047	0.057	0.038	0.000	-						
35	*H. granulata* 1	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	-					
36	*H. granulata* 2	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	0.000	-				
37	*H. granulata* 3	0.066	0.057	0.057	0.066	0.057	0.075	0.075	0.075	0.075	0.057	0.047	0.066	0.058	0.048	0.075	0.075	0.038	0.038	0.038	0.075	0.066	0.057	0.057	0.076	0.067	0.069	0.047	0.047	0.054	0.057	0.066	0.067	0.047	0.047	0.000	0.000	-			
38	*H. fai* 2	0.078	0.076	0.076	0.077	0.068	0.067	0.067	0.067	0.067	0.048	0.058	0.067	0.077	0.067	0.066	0.066	0.048	0.048	0.048	0.078	0.039	0.058	0.058	0.127	0.088	0.089	0.068	0.068	0.095	0.059	0.068	0.059	0.068	0.068	0.067	0.067	0.067	-		
39	*H. pacifica*	0.086	0.096	0.096	0.086	0.076	0.115	0.115	0.115	0.115	0.096	0.086	0.124	0.087	0.077	0.096	0.096	0.077	0.077	0.076	0.076	0.094	0.058	0.058	0.076	0.118	0.120	0.098	0.098	0.109	0.095	0.105	0.105	0.086	0.086	0.057	0.057	0.057	0.117	-	
40	*H. schmardae*	0.077	0.086	0.086	0.076	0.067	0.105	0.105	0.105	0.105	0.105	0.115	0.115	0.097	0.087	0.124	0.124	0.125	0.125	0.124	0.124	0.123	0.096	0.096	0.067	0.098	0.089	0.118	0.118	0.097	0.124	0.133	0.114	0.115	0.115	0.096	0.096	0.096	0.127	0.076	-

Appendix 4.2.5b. Uncorrected 'p' distance matrix at second codon for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-																																							
2	*H. uarnak* 2	0.000	-																																						
3	*H. uarnak* 3	0.000	0.000	-																																					
4	*H. uarnak* 6	0.000	0.000	0.000	-																																				
5	*H. uarnak* 8	0.009	0.009	0.009	0.009	-																																			
6	*H.* sp. A 1	0.000	0.000	0.000	0.000	0.009	-																																		
7	*H.* sp. A 2	0.000	0.000	0.000	0.000	0.009	0.000	-																																	
8	*H.* sp. A 4	0.000	0.000	0.000	0.000	0.009	0.000	0.000	-																																
9	*H.* sp. A 5	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	-																															
10	*H.* sp. A 6	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	-																														
11	*H.* sp. A 7	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	-																													
12	*H.* sp. A 9	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	-																												
13	*H. undulata* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																											
14	*H. undulata* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																										
15	*H. gerrardi* 1	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																									
16	*H. gerrardi* 5	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																								
17	*H. toshi* 1	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																							
18	*H. toshi* 2	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																						
19	*H. toshi* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-																					
20	*H. pastinacoides*	0.009	0.009	0.009	0.009	0.019	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.010	0.010	0.009	0.009	0.009	0.009	0.010	-																				
21	*H. uarnacoides* 1	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	-																			
22	*H.* sp. E 1	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	-																		
23	*H.* sp. E 2	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	-																	
24	*H.* sp. F	0.009	0.009	0.009	0.009	0.019	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.019	0.009	0.009	0.009	-																
25	*H. chaophraya* 1	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	-															
26	*H. chaophraya* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	-														
27	*H. chaophraya* 3	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	-													
28	*H. chaophraya* 4	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-												
29	*H. chaophraya* 6	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-											
30	*H. walga* 1	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	-										
31	*H. imbricata*	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.019	0.010	0.010	0.010	0.010	0.010	0.000	-									
32	*H. oxyrhyncha*	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.029	0.019	0.019	0.019	0.019	0.019	0.029	0.029	-								
33	*H. signifer* 2	0.019	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.019	0.019	0.009	0.009	0.019	-							
34	*H. signifer* 3	0.019	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.028	0.019	0.019	0.019	0.019	0.019	0.009	0.009	0.019	0.000	-						
35	*H. granulata* 1	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.019	0.019	0.019	-					
36	*H. granulata* 2	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.019	0.019	0.019	0.000	-				
37	*H. granulata* 3	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.019	0.019	0.019	0.000	0.000	-			
38	*H. fai* 2	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.019	0.019	0.019	0.000	0.000	0.000	-		
39	*H. pacifica*	0.009	0.009	0.009	0.009	0.019	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.010	0.010	0.009	0.009	0.009	0.009	0.010	0.019	0.009	0.009	0.009	0.019	0.010	0.010	0.010	0.010	0.011	0.019	0.019	0.029	0.028	0.028	0.009	0.009	0.009	0.010	-	
40	*H. schmardae*	0.038	0.038	0.038	0.038	0.048	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.048	0.038	0.038	0.038	0.048	0.038	0.039	0.038	0.038	0.040	0.029	0.029	0.038	0.019	0.019	0.038	0.038	0.038	0.038	0.029	-

Appendix 4.2.5c. Uncorrected 'p' distance matrix at third codon for partial cytochrome *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*H. uarnak* 1	-																																							
2	*H. uarnak* 2	0.000	-																																						
3	*H. uarnak* 3	0.000	0.000	-																																					
4	*H. uarnak* 6	0.104	0.104	0.104	-																																				
5	*H. uarnak* 8	0.113	0.113	0.113	0.009	-																																			
6	*H.* sp. A 1	0.198	0.198	0.198	0.189	0.198	-																																		
7	*H.* sp. A 2	0.198	0.198	0.198	0.189	0.198	0.000	-																																	
8	*H.* sp. A 4	0.198	0.198	0.198	0.189	0.198	0.000	0.000	-																																
9	*H.* sp. A 5	0.198	0.198	0.198	0.189	0.198	0.000	0.000	0.000	-																															
10	*H.* sp. A 6	0.179	0.179	0.179	0.179	0.189	0.094	0.094	0.094	0.094	-																														
11	*H.* sp. A 7	0.236	0.236	0.236	0.226	0.236	0.208	0.208	0.208	0.208	0.170	-																													
12	*H.* sp. A 9	0.189	0.189	0.189	0.198	0.208	0.028	0.028	0.028	0.028	0.085	0.217	-																												
13	*H. undulata* 2	0.182	0.182	0.182	0.161	0.152	0.222	0.222	0.222	0.222	0.201	0.241	0.230	-																											
14	*H. undulata* 3	0.164	0.164	0.164	0.162	0.152	0.223	0.223	0.223	0.223	0.165	0.242	0.212	0.038	-																										
15	*H. gerrardi* 1	0.311	0.311	0.311	0.321	0.311	0.311	0.311	0.311	0.311	0.330	0.321	0.302	0.338	0.340	-																									
16	*H. gerrardi* 5	0.311	0.311	0.311	0.321	0.311	0.311	0.311	0.311	0.311	0.330	0.321	0.302	0.338	0.340	0.000	-																								
17	*H. toshi* 1	0.330	0.330	0.330	0.283	0.274	0.283	0.283	0.283	0.283	0.321	0.311	0.274	0.355	0.337	0.245	0.245	-																							
18	*H. toshi* 2	0.330	0.330	0.330	0.283	0.274	0.283	0.283	0.283	0.283	0.321	0.311	0.274	0.355	0.337	0.245	0.245	0.000	-																						
19	*H. toshi* 3	0.349	0.349	0.349	0.302	0.292	0.302	0.302	0.302	0.302	0.340	0.330	0.292	0.366	0.358	0.264	0.264	0.019	0.019	-																					
20	*H. pastinacoides*	0.330	0.330	0.330	0.302	0.311	0.311	0.311	0.311	0.311	0.311	0.264	0.302	0.403	0.385	0.292	0.292	0.274	0.274	0.292	-																				
21	*H. uarnacoides* 1	0.292	0.292	0.292	0.292	0.283	0.255	0.255	0.255	0.255	0.292	0.255	0.245	0.308	0.310	0.283	0.283	0.264	0.264	0.283	0.321	-																			
22	*H.* sp. E 1	0.264	0.264	0.264	0.226	0.236	0.311	0.311	0.311	0.311	0.274	0.274	0.321	0.310	0.311	0.292	0.292	0.292	0.292	0.311	0.274	0.283	-																		
23	*H.* sp. E 2	0.264	0.264	0.264	0.226	0.236	0.311	0.311	0.311	0.311	0.274	0.274	0.321	0.310	0.311	0.292	0.292	0.292	0.292	0.311	0.274	0.283	0.000	-																	
24	*H.* sp. F	0.406	0.406	0.406	0.396	0.406	0.377	0.377	0.377	0.377	0.377	0.330	0.387	0.401	0.384	0.396	0.396	0.406	0.406	0.406	0.387	0.368	0.311	0.311	-																
25	*H. chaophraya* 1	0.268	0.268	0.268	0.287	0.297	0.335	0.335	0.335	0.335	0.315	0.277	0.325	0.301	0.323	0.316	0.316	0.364	0.364	0.354	0.344	0.306	0.296	0.296	0.279	-															
26	*H. chaophraya* 2	0.251	0.251	0.251	0.271	0.281	0.319	0.319	0.319	0.319	0.300	0.280	0.309	0.285	0.306	0.262	0.262	0.348	0.348	0.339	0.367	0.310	0.339	0.339	0.302	0.049	-														
27	*H. chaophraya* 3	0.264	0.264	0.264	0.255	0.265	0.321	0.321	0.321	0.321	0.302	0.264	0.312	0.298	0.319	0.312	0.312	0.330	0.330	0.321	0.331	0.312	0.283	0.283	0.322	0.146	0.118	-													
28	*H. chaophraya* 4	0.264	0.264	0.264	0.255	0.265	0.321	0.321	0.321	0.321	0.302	0.264	0.312	0.298	0.319	0.312	0.312	0.330	0.330	0.321	0.331	0.312	0.283	0.283	0.322	0.146	0.118	0.000	-												
29	*H. chaophraya* 6	0.383	0.383	0.383	0.382	0.381	0.384	0.384	0.384	0.384	0.365	0.311	0.375	0.347	0.369	0.276	0.276	0.376	0.376	0.366	0.383	0.230	0.343	0.343	0.338	0.234	0.205	0.245	0.245	-											
30	*H. walga* 1	0.349	0.349	0.349	0.340	0.330	0.311	0.311	0.311	0.311	0.330	0.311	0.321	0.362	0.364	0.358	0.358	0.302	0.302	0.311	0.387	0.264	0.340	0.340	0.340	0.317	0.308	0.331	0.331	0.299	-										
31	*H. imbricata*	0.358	0.358	0.358	0.330	0.340	0.330	0.330	0.330	0.330	0.340	0.358	0.349	0.410	0.393	0.387	0.387	0.340	0.340	0.349	0.377	0.292	0.311	0.311	0.330	0.308	0.299	0.341	0.341	0.281	0.142	-									
32	*H. oxyrhyncha*	0.302	0.302	0.302	0.292	0.302	0.292	0.292	0.292	0.292	0.330	0.330	0.302	0.380	0.391	0.425	0.425	0.368	0.368	0.358	0.396	0.302	0.302	0.302	0.387	0.345	0.331	0.388	0.388	0.385	0.226	0.198	-								
33	*H. signifer* 2	0.283	0.283	0.283	0.292	0.302	0.264	0.264	0.264	0.264	0.302	0.292	0.274	0.347	0.368	0.340	0.340	0.321	0.321	0.330	0.358	0.274	0.264	0.264	0.396	0.316	0.326	0.311	0.311	0.349	0.274	0.226	0.208	-							
34	*H. signifer* 3	0.292	0.292	0.292	0.302	0.311	0.274	0.274	0.274	0.274	0.311	0.302	0.283	0.338	0.358	0.349	0.349	0.330	0.330	0.340	0.368	0.283	0.274	0.274	0.387	0.325	0.336	0.321	0.321	0.359	0.283	0.236	0.217	0.009	-						
35	*H. granulata* 1	0.330	0.330	0.330	0.340	0.349	0.340	0.340	0.340	0.340	0.321	0.377	0.349	0.354	0.356	0.321	0.321	0.387	0.387	0.387	0.387	0.311	0.330	0.330	0.340	0.310	0.275	0.305	0.305	0.290	0.321	0.292	0.340	0.283	0.292	-					
36	*H. granulata* 2	0.321	0.321	0.321	0.330	0.340	0.330	0.330	0.330	0.330	0.311	0.368	0.340	0.344	0.346	0.311	0.311	0.396	0.396	0.396	0.396	0.302	0.321	0.321	0.349	0.300	0.265	0.314	0.314	0.279	0.311	0.283	0.330	0.292	0.302	0.009	-				
37	*H. granulata* 3	0.321	0.321	0.321	0.330	0.340	0.330	0.330	0.330	0.330	0.311	0.368	0.340	0.344	0.346	0.311	0.311	0.396	0.396	0.396	0.396	0.302	0.321	0.321	0.349	0.300	0.265	0.314	0.314	0.279	0.311	0.283	0.330	0.292	0.302	0.009	0.000	-			
38	*H. fai* 2	0.265	0.265	0.265	0.256	0.266	0.199	0.199	0.199	0.199	0.256	0.303	0.208	0.289	0.328	0.389	0.389	0.331	0.331	0.341	0.340	0.246	0.218	0.218	0.379	0.337	0.341	0.324	0.324	0.346	0.285	0.275	0.256	0.190	0.199	0.294	0.284	0.284	-		
39	*H. pacifica*	0.415	0.415	0.415	0.406	0.396	0.415	0.415	0.415	0.415	0.415	0.425	0.415	0.402	0.424	0.415	0.415	0.406	0.406	0.406	0.443	0.387	0.368	0.368	0.406	0.387	0.383	0.373	0.373	0.410	0.368	0.358	0.349	0.358	0.368	0.358	0.358	0.358	0.390	-	
40	*H. schmardae*	0.435	0.435	0.435	0.482	0.492	0.416	0.416	0.416	0.416	0.416	0.407	0.397	0.451	0.454	0.454	0.454	0.435	0.435	0.436	0.454	0.388	0.388	0.388	0.369	0.397	0.419	0.411	0.411	0.428	0.378	0.340	0.369	0.359	0.350	0.378	0.378	0.378	0.381	0.219	-

Appendix 4.2.6. Molecular phylogenetic tree scores of parsimony analyses using various weighting schemes for partial 16S and cytochrome *b* sequence data sets.

Gene; weighting (number of tree(s) retained); consensus type	Consensus tree length	Consistency index (CI)	Retention index (RI)	Rescaled consistency index (RC)
A. 16S				
unweighted (10,039 trees)				
Strict	577	0.445	0.669	0.298
50% majority rule	508	0.506	0.740	0.374
Ti:Tv (2:1) (9,000 trees)				
Strict	484	0.525	0.775	0.407
50% majority rule	478	0.531	0.781	0.415
Ti:Tv (1:0) (18,600 trees)				
Strict	142	0.401	0.548	0.220
50% majority rule	108	0.528	0.729	0.385
B. cytochrome *b*				
unweighted (10 trees)				
Strict	510	0.359	0.666	0.239
50% majority rule	495	0.370	0.681	0.252
Ti:Tv (6:1) (4 trees)				
Strict	551	0.388	0.687	0.267
50% majority rule	551	0.388	0.687	0.267
Ti:Tv (1:0) (1,293 trees)				
Strict	78	0.590	0.673	0.397
50% majority rule	69	0.667	0.765	0.510
1st and 2nd codon (30 trees)				
Strict	94	0.511	0.747	0.382
50% majority rule	90	0.533	0.769	0.410
Ti:Tv (9:1) at 3rd codon (1 tree)				
single tree scores	852	0.488	0.725	0.354
Ti:Tv (1:0) at 3rd codon (1,382 trees)				
Strict	169	0.467	0.651	0.304
50% majority rule	145	0.545	0.744	0.405
Ti:Tv (3:1) at 1st codon (6 trees)				
Strict	522	0.372	0.679	0.252
50% majority rule	510	0.380	0.691	0.263